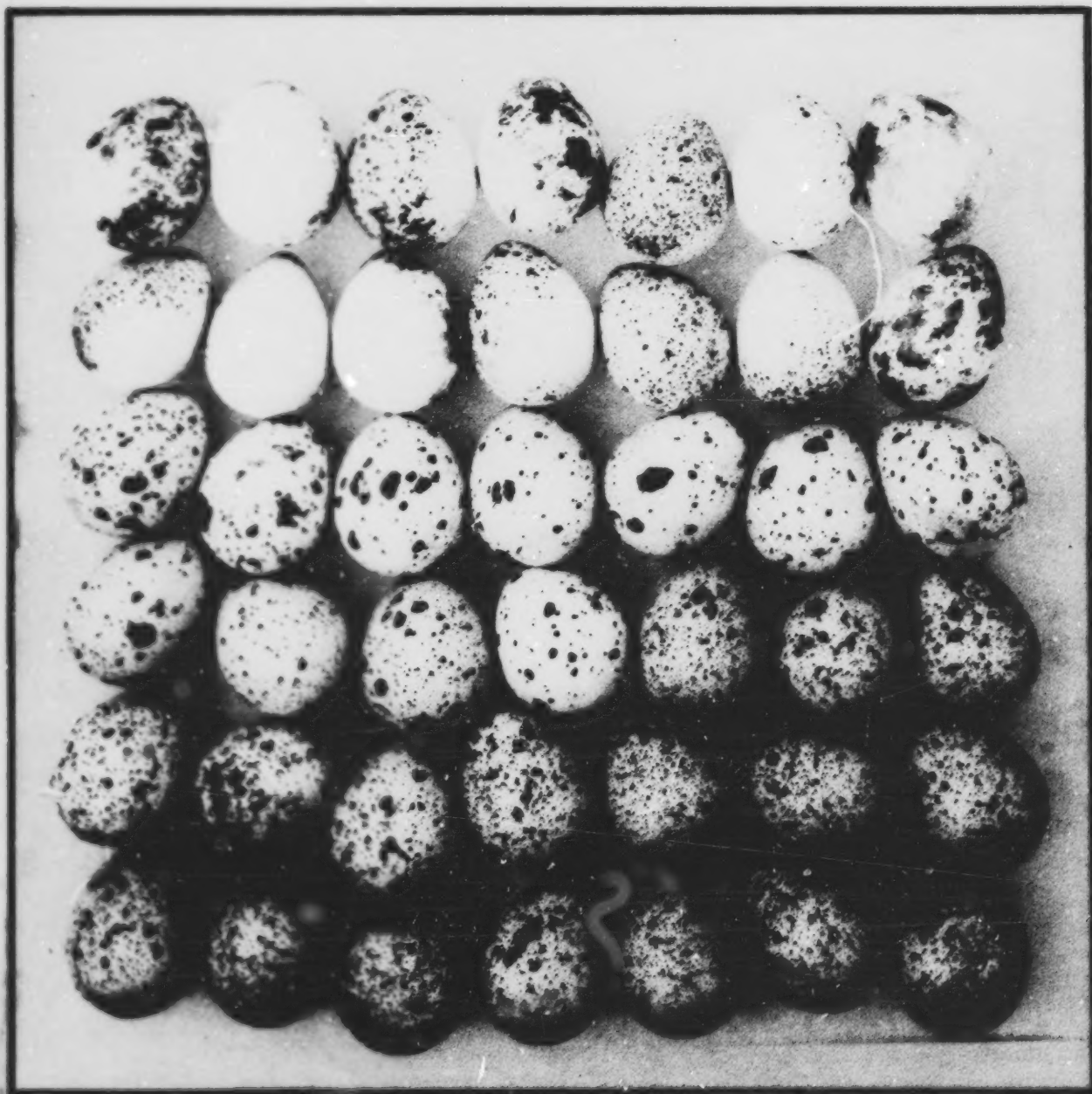


British Columbia Provincial Museum
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Museum Collections: Their Roles and Future in Biological Research

E.H. Miller, Editor



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**Occasional Papers
of the
British Columbia Provincial Museum
No. 25**

***Museum Collections:
Their Roles and Future
In Biological Research***

**E.H. MILLER
Editor**



Province of British Columbia
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PREFACE

In January 1982 Yorke Edwards, Director of the British Columbia Provincial Museum, encouraged his staff to reflect on objects as the essence of natural history museums, and on their conventional and untapped uses in education, display, and research, with an eye to publishing individual or collected papers on the topic. He did not have preconceived answers to problems of interpretation of natural history specimens or of research on them, but had long recognized that major problems in both areas existed; for example, museum displays in natural history typically are "fakery made as realistic as possible" (Edwards 1979:16) and techniques of preparing scientific specimens have "remained largely in the 19th century" (Edwards 1979: 15). If the latter is true, has research in natural history museums just "adapted to . . . inadequate specimens" (Edwards 1979:15), or has it simply progressed and moved away from the use of specimens as a primary source of information? I believed that the truth lay between and that the subject had been discussed inadequately, so suggested to Yorke that we publish a volume focussing on actual and potential uses of natural history specimens in research. This seemed appropriate in light of his January remarks, and in considering the sudden surge of interest and conflicting judgements on research collections in general, and on ornithological collections in particular (Foster 1982; Barlow and Flood 1983).

I intended this volume to be a comprehensive collection of writings on the past, present, and future uses of museum collections in biological research. Expectedly, it is less even and comprehensive than hoped for, with glaring omissions in such areas as wildlife research, parasitology, prokaryote systematics, *etc.*, and a bias toward ornithology (see Banks 1979). Even so, the volume brings together ideas, criticisms, and observations from an array of disciplines, and I hope these will contribute to an ongoing, constructively critical view of the role of research specimens in research by museum and non-museum biologists.

Yorke Edwards presents an overview of museum research, as seen by a naturalist-turned-administrator (Chapter 1). Bob Ogilvie discusses the scope of conventional botanical collections (Chapter 2), and Bill Berry emphasizes the continued importance of touchstones in biological collections (Chapter 3; I wonder what fraction of graduating biology majors can explain the type concept these days?).

Evolutionary concepts applied to growth and molecular evolution are changing rapidly; the relationships of collections to research in those areas are thoughtfully treated by Pere Alberch (Chapter 4) and George Barrowclough (Chapter 5). Changing equally fast is our understanding of microevolution and geographic differentiation, and statistical and mathematical applications to their study; Allan Baker provides a fine review (Chapter 6).

Approaches to biogeographic research are in ferment, but Adolf Ceska adroitly avoids the issues and focusses discussion on "conventional" phytogeography, with emphasis on British Columbia (Chapter 7). Richard Hebda similarly avoids the tangle of macroevolution, phylogenetic inference, *etc.*, and presents a far-reaching review of paleobiology (Chapter 8).

Morphology retains a central place in collection-based research, but increasingly demands higher-quality specimens, and more care and thought in their study. Bob Raikow and Walter Bock discuss these and related topics in their constructive and provocative chapters (9, 10).

Museum collections can provide useful information to ethologists (see my Chapter 11), and should be augmented routinely with specimens acquired in ecological research or during surveys of environmental assessment/impact/*etc.* (Ralph Brinkhurst, Chapter 12). Gerry Allen and Rob Cannings explore many avenues in pointing out the wealth of information which can be extracted from specimens for life-history studies (Chapter 13), and John Fitzpatrick stresses the inseparability of field and museum components to research in ecomorphology (Chapter 14); these two important chapters underline repeatedly how much innovative research can be carried out on existing collections, and can provide an impetus for future collecting.

No book concerned with how remnants of life can be viewed and studied is complete without reference to the role played by living collections (Peter Ashton, Chapter 15). Finally, Henri Ouellet wraps up the book with an historical look, and a plea for more extensive and purposeful scientific collecting (Chapter 16).

I wish to thank Yorke Edwards for the initial impetus to undertake the preparation of this book, and for continued encouragement. The contributors to the book have been prompt and patient, and I appreciate their care in preparing chapters and in responding to my questions. Finally, I am grateful to Rob

Cannings for numerous discussions; to Lynne Macdonald and Phil Nott for technical assistance; to Earl Godfrey for introducing me to museum collecting and collections; and to Stu Macdonald, for teaching me to use museum specimens in trying to understand living organisms.

Victoria
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Edward H. Miller

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**The investment of human energy in the formation
and maintenance of a research museum is
justified only in proportion to the amount of
real knowledge which is derived from its materials
and given to the world.**

Joseph Grinnell, in
The Museum Conscience

1. RESEARCH: A MUSEUM CORNERSTONE

R.Y. EDWARDS

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I. INTRODUCTION

Introductions such as this can take many appropriate directions. In this case my experience as a manager of museums has influenced my choice to discuss research done on museum collections in the context of what a museum really is, and what a museum is supposed to do.

Most people who think that they understand museums do not, for they have only partial understandings, a condition found even within the staffs of museums themselves. My message here is therefore about the museum's preoccupation with the gathering and distribution of information, which is the museum's ultimate purpose.

The hunt for information brings research into museums in its role of increasing understanding of the museum's collections. While its functional focus may not always be on the collections themselves, its purpose must always be related to them, and to the museum's mandate to increase its knowledge about them.

The physical heart of a museum is its collection, in fact having a collection is what makes a museum a museum, and most activity in most museums is involved with the acquisition, care, understanding, and use of their collections (Fig. 1; MacBeath and Gooding 1969; Alexander 1979). Three aspects of museum collections are explored in this chapter: they are cultural treasures of high value; this treasure can be quite vulnerable to destruction and so needs special care; and the high values preserved are related mainly to the information content of objects. The museum's medium is the object; the object is the museum's message (see McLuhan 1964). Hence museums are information banks, these banks need special protections, and the objects in the collections contain primary information to be held, protected, studied and communicated about to society.

The notion that objects contain information is not acceptable to everyone, but when one considers humans as biological sensory machines an object contains nothing else. Our nervous systems can turn a bird or a cup, or portions of them, into verbally communicable information; nevertheless, without us nearby such things hold information just as surely as does a book that has not been read.

The word "information" used here and throughout this chapter therefore includes both known information (which my dictionary equates to "data," "facts," and "knowledge") and undiscovered or potential information. In museum management both kinds of information are of major concern. It is the sum of the two that makes the cost of museums acceptable to society, and so makes museums possible. And it is the confidence that efforts in the museum to find and communicate unknown information will often succeed that makes the cost of research acceptable, indeed essential to the success of the museum.

Many kinds of information exist in museums: the shapes given the human form by Picasso; the colours of Greek vases; the evident technology of stone weapons; the structures of bats' wings. Much of it is old knowledge to mankind, but each of us can discover it anew for ourselves as information in its primary form. This personal discovery in the museum's galleries is perhaps the most important direct contribution of the museum to society, since a large audience is presented with the display of a large number of objects otherwise not easily available for inspection and study, and the result in the galleries is a large daily quota of personal discovery. Labels and expert people can of course enlarge the individual's depth and range of discovery. All of this is the most important part of the museum's communication of known information. In order to have fresh and accurate information to communicate, the museum itself is on a constant exercise of discovery in its offices and laboratories. This research into the unknown may or may not be sophisticated, and most often is not, because most museums are small and unsophisticated. Research in museums to increase knowledge of collections seems to be a naturally spontaneous result of combining

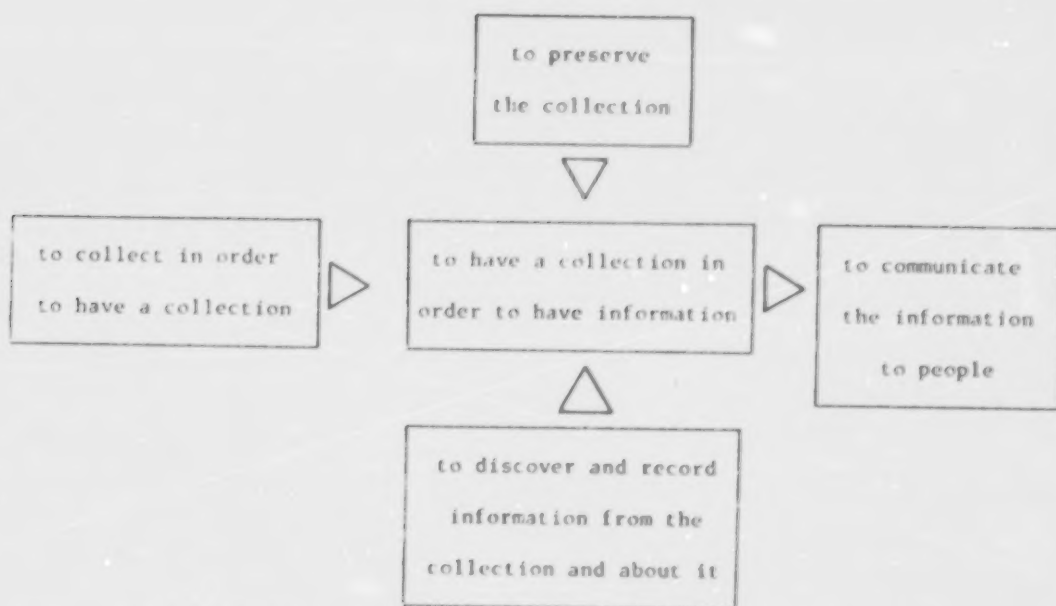


Fig. 1. Relationships among the five main objectives of museums (see text for explanation).

human curiosity with collections of unusual things. Whether focusing on the shapes of wooden bowls or on trace elements in falcon feathers, research reveals potential information, all of it useful to museum audiences, some of it eventually improving the world's textbooks. The museum's preoccupation with collected objects is to the end, eventually, of assisting the objects to pass on information to people. All other reasons are incidental.

The study of museum collections is essential to the successful survival of museums (Parr 1955; Finlay 1977). It is the creative endeavour producing new information which has always been the museum's major contribution to mankind. In contrast, the museum's educational functions are better known because they constantly touch the public. The exhibits, lectures, publications, and other voices of the museum are popular, and fortunately are also widely regarded as contributions to society valuable enough to justify the costs of having museums. Here is a case of the delivery system attracting most of the support, while the creative source of the goods delivered receives small encouragement. Often research is even challenged as a necessary function of museums (Burcaw 1975).

Anyone whose daily view is from a position overlooking an entire museum of some size lives with a remarkable and quite apparent public misconception. Most people believe that a museum is simply the display galleries themselves, when in fact the foundations and strengths of major museums are the collections which are largely unavailable to the casual visitor.

In large museums, even senior staff in specialized positions can have surprisingly fragmentary understandings of the relative importance of the museum's many functions. Where I work I am often reminded of the old Hindu tale of the blind men who approached an elephant to understand this famous animal. One advanced with outstretched hands to encounter the animal's side, and he at once proclaimed the elephant to be like a wall. Another, seizing the trunk, knew the elephant to be like a snake. A third chanced onto a sturdy leg and knew the elephant was like a tree. An ear convinced another that it was like a large leaf, while the tail in another's hands was proof that it was like a rope. Yet another found a tusk to be obviously a sort of spear. Arguments of course ensued, for each was partly right, but all were mostly wrong.

The staff in a large museum is rather like these Indians, each person in touch with a specialized museum function, each largely uninformed about other parts quite accessible but seldom visited or even discussed with others.

It is difficult to fit a numerous visiting public into the old story but, alternatively, if thousands of visitors were to file past a dark window from which protruded the trunk of an elephant otherwise invisible inside, the thousands would all have a concept of the object called elephant that was quite fragmentary and misleading.

Visitors constantly filing through the galleries of large museums do not see the museum at all, although most are convinced that they do. Where I work most of these visitors experience only a few of some 25 methods used by the museum to communicate with the public, and they see perhaps three per cent of the museum's collections. While the exhibits are unique and at times a spectacular experience, still the visitor sees no hint of the museum's large storage areas stuffed with collections, attended by keepers caring for them and by scientists and scholars studying them. The basic museum is hidden; they see only a small and not necessarily representative sample of the collection, yet *that* — the collection — is the museum, hidden to most.

My constant reminder of this incomplete understanding is the people who stumble onto the fact of the large and somewhat inaccessible collections when in conversation with me about my work, and in astonishment they almost always say the same thing: "But what good are they if we all can't see them?" Here in a nutshell is the museum's great vulnerability. The public believes that their cultural treasure-houses are simply pleasantly informative exhibition centres with their most important spaces available to all.

The curator, not the exhibition designer (and certainly not the director), is therefore at the heart of the museum, improving the collection, protecting it, studying it to discover what information the objects hold. In small museums the curator must often do what he can of all three — and more if he is the total staff. Large museums, in contrast, have a number of curators who may specialize in one of collections care, research, communications, or other functions. Large or small, however, a museum with no inquiring mind constantly asking questions of the collection — and working effectively at answering them — is a dead museum. The collection must speak, and in a lively manner.

II. THE WORTE OF MUSEUMS

Civilized people like museums (I say this while preferring the vernacular meaning of "civilized." Perhaps a more enlightened word would be "westernized," there being some doubt about who if anyone is civilized). This love affair with museums exists not just because some objects in some museum collections are worth a lot of money, but because people concerned with their past and their place in the present regard museum collections as intrinsically worthwhile. In short, they are valuable. This reverence for museums is found at all levels of sophistication in people, and is held for museums at all levels of affluence and support. Huge national museums may be those best known, but they are few compared to the thousands of small museums in the towns and villages of many nations. These small ones demonstrate best the universal human dedication to museum values. People simply want museums in their communities. If they are not given them, they create them.

The citizen-turned-tourist carries the same dedication on his travels. Famous museums in distant places are given top priority on the traveller's list of sights that must be seen. Often these are essential objectives because they are the accepted places to see ("My dear, you were in Paris and didn't see the Louvre?). But fortunately not all try to "do" the Louvre in twenty minutes. Those who try are at the edges of cultural interest, uncertain about the attraction but sure of the social implications. Obviously part of the value is in others knowing about our interest.

The public's unstated but abundantly demonstrated acceptance of the high value of museums is not widely understood. It is usually just assumed. A close look at the assumption reveals often that museums are simply viewed as good for the "tourist industry," which of course they are but are much more as well. On another level of monetary values, some museums pay huge sums for old — and not so old — art, and this can distort opinions on why museums are considered treasure houses in the naive sense of "jewels and gold and rare old paintings." Even highly placed people within museums can have this problem, which is the not uncommon condition of knowing more about price than value. From this strictly monetary position, I suggest one must wonder why society considers paying out a million dollars for a painting to be a benefit and not a drain. The price is surely paid to obtain value of considerable proportions.

Most kinds of museum collections contain objects predominantly of no special commercial interest. Stone chips from an archeological dig, pickled fish from a local shore, things like these dominating museum collections have essentially no dollar value in any established market place. In the properly functioning museum, the "expensive" and the "cheap" in the collections are both there for the same reason, which is that they are carefully selected for their content of tangible information; and information has supreme value. It was information that got us out of our hiding places in caves to eventually stand on the Moon. The leap for some of us took only about 15,000 years, a mere tick of Earth's geological clock (albeit that others of us, still in the stone age, have not yet begun the jump). The pace of this accumulation of information has been increasing with long pauses for millions of years, for it was a very long evolutionary and cultural climb to the comfort of a fire in a cave. Currently we are experiencing an unprecedented information explosion which seems much more quantitative than qualitative.

Information is survival, power, and entertainment, so information is valuable. From its discovery can come new technological invention. More rarely it reveals revolutionary insights to enrich the inner man.

In the beginning, the accumulation and passing on of information began its long evolution toward modern education. This produced the school textbook, the modern Aladdin's lamp granting to each generation its wishes to know what others know. Accurate information is by far our most valuable personal resource; it is the secret of our present commanding domination of this lovely and lively green planet, a fact in no way challenged by our obvious lack of wisdom in keeping it lively, and so lovely.

We live in a constant bombardment of information and have done so since our ancestors first had nervous systems in touch with their surroundings. Our senses are constantly reporting informative messages. Almost always there is too much for us to receive, so our receptions are turned off; but more commonly we do not know enough to recognize most messages available and receivable as even being there. To illustrate the first case, we may not see friends among people passed on a crowded street because we are accepting everyone together as a faceless crowd; while in the second case a mushrooming dark cloud in the distance means only what we see, until we learn that it means a thunderstorm as well. On a museum level, we do not at first see the scratches on an ancient stone tool at all, later we do not regard them as being information about the history of the tool, but research may reveal the scratches to be the most meaningful and informative part of it. What most people would not see, and a few would see but dismiss as meaningless, can hold information worth a standing ovation at a conference of anthropologists. Tenacity and a good inquiring mind can make startling sense out of the meaningless. Casual experience furnishes most of our first hand learning, but a deliberately organized hunt — research — must ferret out the more hidden truths that are all about us.

Before Francis Bacon, Europe mouldered mentally in its middle ages, its leading minds firmly controlled by Greek ancients long dead who left behind an uncertain wisdom of facts and rare insights liberally mixed with half truth and nonsense. Bacon was at the turning point, directing thought away from past authority toward personal observation and a scientific system of collective observation and verification (Eiseley 1973). Travellers, both the physical and mental kinds, then became suspect until their tall tales were convincingly verified. The new idea was a simple one, namely looking at the real thing at first hand and arranging (as through publishing) for others to verify what was found. Briefly stated, the new approach recognized that the grass is the only reliable authority to consult on why the grass is green.

The unique strength of the museum in our society results from this powerful concept. Museums, by collecting objects, hold the information held by real things. That information may be about man or nature or both, and may relate to art, history, or science. At museums people can ask the old vase for centuries not just about its more obvious colours and textures, curves and spatial harmonies, but also where its clay was dug, the nature of its pigments and glazes, how it was shaped and fired, what it was used for, perhaps even who used it, and whose hand brought it into being, and where. In a way, the object speaks to those able to translate. Self-appointed experts can guess endlessly at the more hidden facts, but the reliable expert can prove what he knows to others.

Even in these enlightened times, however, people seem largely unable to understand the planet that supports them or the cultures that control their lives and those of others. In spite of the scientific revolution which Francis Bacon helped to start around 1600, many of us are still prone to believing nonsense as fact, which perhaps suggests that we have not changed much in 400 years. Also, we are still educated predominantly by accepting the word of authority, mostly in books, but by spoken word and man-made picture as well. Therefore much of what most of us think we know is probably nonsense, still. We accept

someone else's fallible word for most of what we think we know of human knowledge. In fact most of us are now urbanites who experience to verify as true far less of the world, its life, and man's place in it, than most people did in Bacon's time. The city is a man-made environment, a hugely successful retreat overflowing with people escaping from the more natural, less comfortable environments that sustain us. For all its obvious benefits the city encourages a dangerous ignorance of human roots and human ecology. The museum is one of our few antidotes to these vacancies in the intellect, for it attracts people to first hand enlightenment on Earth history and Earth ecology.

While the museum's unique value to society is based on its collections and their store of information, there are of course other "values." Its objects may have market values, its doors may yield admission revenues, its lands and buildings and equipment have capital values. The staff spends wages that boost the local economy, citizens find pleasure and entertainment values in the galleries, tourists are attracted and stay longer to spend money locally, volunteers find priceless new dimensions in their lives, and children discover new horizons open to them in education and life. These and more are part of a good museum's worth. The supreme value, however, is in the basic purpose of the museum, in its mandate to save things valuable as information, its mandate to discover hidden information in those things saved, and its mandate to communicate what it knows to people as palatably as is possible.

Except for the process that created Man, and for Earth's green skin of life which produced and sustains him, nothing in Man's history has proven more important to him than knowledge, which requires discovering to exist, then requires passing on to be generally useful. Good museums do these things. Discovering is the essential creative act in this process; research is sophisticated discovering.

III. PROTECTING THE INFORMATION

The very foundation of museum research is a collection well selected as to probable value and well cared for so in good condition.

Valuables require protection. Museum collections are continuously at risk, so constant surveillance and frequent removal of hazards are required. In responsible museums good conservation and security practices are in place as a necessity to ensure the prolonged survival of the collections. If they are not worth such special efforts to protect them, they are not worth collecting in the first place. Keeping them is therefore irresponsible expense.

In museums, objects are saved to preserve the information that they contain. This information is not just in their obvious shapes, colours, textures, weights, and adherents, it is also in the skillful interpretation of the object's chemistry and structure, in its imperfections and evidence of deterioration, and sometimes in hidden adherents or impregnations that result from the object's past experiences.

The curator with skills in reading these messages may become a completely specialized scientist, but this is not to be taken as the norm. Usually curators can be only partly so specialized in their work, for most of them work in small museums. In large museums curators may specialize almost completely in one or the other of their traditional roles, but at the same time these specialists must not lose sight of the essential role of the curator as the main figure responsible for the quality of the museum's functions of collecting, preserving, studying and communicating. Above all else, the curator is the collection's accountable keeper, expert manager, and accomplished interpreter of its messages.

Given the collection in its given state, which is the result of past events, collection care is a current activity reflecting curatorial competence within the limits of the fixed conditions affecting it.

Today's quality of collection care can be very uneven from place to place and, as in all keepers of anything, the curator in charge is potentially the collection's worst enemy. Preoccupation with other things, or inertia, can allow correctable hazards to result in severe damage, while damaging treatments can destroy much of the information originally contained by the objects. Not all hazards come directly from the curator however. Changeable physical and chemical conditions of storage can be destructive influences. Heat, moisture and light can be damaging. Living organisms can disfigure or even destroy many kinds of objects. Staff carelessness is a constant risk, and may reflect lax policies including lack of training in the handling of objects. While collections are meant to be used, there must be control and training of those users who are not staff, as well as emphasis on kinds of uses permitted for staff on the one hand and outsiders on the other. Also, a good management system must keep track of where objects are located when in or out of their usual storage places, and if out when they will be returned.

My lifetime of intermittent field collecting, museum haunting, curation and museum management has revealed a dreary list of disasters in collections best not documented here, but clearly the hazards to biological specimens especially are effective and many, and they can strike quickly between inspections. Here the attitudes and concerns about protection held by the persons responsible for collections can loom large as factors ineffective at preventing disasters. Perhaps biological specimens both inside and outside the museum are more vulnerable than most museum objects, but there is a contributing factor within the curators themselves. Not uncommon among them is a partial lack of concern for the welfare of the specimen based on the mistaken belief that specimens are easily replaced. This is simply not true. This is unacceptable ignorance of the uniqueness of the individual organism, and an unacceptable contradiction of the museum's essential image as careful keeper of the public's carefully chosen collections. Laxity in collections care is always unacceptable. Any discipline's suggestion for any collection that second or third rate care is good enough must have careful examination by museum administrations, disciplines involved, and the public owner before the thought can have the slightest influence on museum practice.

Human error concerning collections is not confined to curators. Managers of museums and other institutions keeping collections are no less dangerous. Staff changes, a shift in policy, or monetary problems can result in collections lovingly built by enthusiastic specialists receiving no care at all. Wet collections then dry out; dry ones are consumed by organisms. Two personal experiences vividly illustrate this problem. My own small collection of mammals lay neglected in a bedroom drawer during a busy season of sandlot football, and I can remember my astonishment and dismay at discovering hairless specimens resting on liberal sprinklings of sand-like insect droppings. More recently a pioneering collection of hydroids containing many type specimens arrived at a Canadian museum after years of neglect on a university campus. The collector, a professor and authority on this little known group of animals, had cared for his incomparable collection into retirement, but when he died no one was concerned enough to arrange for the care of the collection, or better to send it where it would be appreciated professionally. The collection soon dried to become in many cases specimens of little value, a sad commentary on our academic tunnel vision and on the narrowness of our ethics and concerns. This destruction of abandoned collections can occur in museums too for much the same reasons, but campus collections seem more prone to these unfortunate disintegrations from neglect.

In recent decades, changes in the academic focus of biology departments in universities almost everywhere have increased this problem of the systematic collection at risk. More recently monetary problems have magnified this risk. The campus focus of preference on biological research can range widely through time, the academic interest and the funds to indulge it tending to collect around areas with exciting recent breakthroughs. Currently, cellular and chemical biology are overwhelmingly popular, with the lab down the hall from the Zoology or Botany office the main centre of action, and sometimes able to produce good papers with remarkable frequency. Meanwhile, the biologist out in the weather concerned with whole organisms in wild places is invisible to the indoor crowd, while his kind on campus has become endangered along with the funds available to nourish his research (Edwards 1979b). Such changes in popularity have been not uncommon within all the sciences through much of their histories. In this case the abandonment of taxonomic and systematic studies on campus is hardly related to a lack of useful work to be done since half the world's forms of life have yet to be named (Foster 1982). It will be fortunate if taxonomists can name half of these before they are destroyed, extinct because their ecosystems were destroyed.

Studies of organisms in general and their classification in particular are not only scarce on campuses and in the grants lists. Misguided museum biologists have joined the rush sufficiently to believe in a declining usefulness of museum collections. Museums have always been bastions of work in biological classification. Now they are needed more, not less, as campuses increasingly ignore their responsibilities to the world's forms of life. Unfortunately the universities are opting out just when they are needed most. The process of naming organisms so we can know what we are talking about, and who our fellow space travellers are, is incomplete almost everywhere; the need to identify organisms in unprecedented numbers was never greater for a bewildering number of applied research studies, ecological impact studies, feasibility studies, and renewable resources studies of many kinds (see Chapter 12). As a result taxonomy has gone partly commercial, the incompleteness of world knowledge and the scarcity of skilled taxonomists combining now with some commercial haste to present an interesting basis for inaccuracy. Recently there passed through my town the story of a small research project which involved simply sending the same specimens to a number of commercial laboratories for identification. The opinions received

were unacceptably variable. The best of scientists may disagree on identifications of organisms, but inexperience and haste can produce quite another magnitude of confusion. This problem enlarges at all levels of competence when incomplete research has left unknown species to frustrate the identification process.

The retreat of the universities from biological concern for Earth's unique environments, with their arrays of apparently improbable life forms, is especially threatening to biology's efforts to understand this speck in space where we live, how life helped to construct where we live, or why it needs some protection; and this is because the viewpoints of universities on such matters tend to dominate the university-oriented public agencies that control the grants for biological research.

In museum biology a current debate on the future usefulness of collections of birds is a highly visible result of these current trends in biology, and one which will influence popular opinions on other kinds of biological collections as well. While some curators and other scientists are suggesting the usefulness of bird collections to be largely passed (Ricklefs 1980), legions of amateur enthusiasts in love with the living bird are quite sure of it. Neglect of collections can thrive in such a climate. The situation is not really new, however, for I am reminded of the physicists early in this century who were declaring their science to have finished its work because physics had exhausted its field. In truth, of course, it had hardly got out of the clutches of old Aristotle.

Ironically, while this goes on the science of birds is in some systematic disarray and in need of much research, according to Olson (1981) and McKittrick (1981) among others, and there is also much new ecological information to be gained from old collections (Olson 1981).

Another influence, unusual in biology but operating strongly in ornithology, affects current thinking in the avian discipline. Many ornithologists are now amateur birders metamorphosed into scientists. Their overwhelming concern is the wild bird in its environment, and this influence is large enough to make ornithology in many universities a unique exception to the general trend in biological science toward lab research. Field ornithology is vigorous and impressively productive on many campuses. To these scientists the excitement of birds rarely extends to rows of specimens on museum trays (Ricklefs 1981), yet the basis of their work is the art of identifying birds in the field, which countless specimens collected over more than a century have made possible. The evolution of the modern field guide through Chapman (1911), Seton (1903, 1941), Reed (1906), Hoffman (1927), Taverner (1939), Peterson (1934) and others is a museum achievement perfected in the field, first with the shotgun, then with optical assistance and good reference books. The old science, still with a long way to go, spawned the new art now practiced by millions throughout the westernized world. It will be loaded specimen trays again that help to extend this art into new geographic areas, and into new skills for identifying ages, sexes, and geographic variations.

Systematically organized collections will always be at the cutting edge of biological research, yet not always obviously so, but there of necessity because if you don't name it correctly, you don't know what you are talking about.

Museum collections need more thoughtful, more skillful and more reliable care from curators and museum managers. They are far too valuable to abandon or neglect, or to risk in any way. Future research will need them. There is nothing second rate about the biological specimen as compared to the artifact in history or anthropology. The species represented in museums are at least as valuable as anything else museums collect, for not much on Earth can be more valuable than its forms of life, and we have hardly begun to examine these collections for the information that they contain.

IV. THE OBJECT AS INFORMATION

The normal reaction upon seeing a noteworthy object is to put it into some kind of context. A teapot may transport you to an aunt's living room; a ponderosa pine takes me to golden grasslands on rolling hills. If there is something unusual about the pot or tree, however, the mind will behave differently, concentrating upon the unexpected feature, but usually people see things in an almost generic sense, content to let a teapot be just a teapot, a tree just a tree. This is a kind of self defence, for it would be exhausting to go through even an hour of dwelling carefully on the details of each successive object that the eye encountered. At the same time, most people consider themselves expert on one or two kinds of objects. It may be brands of beer, varieties of daffodils, patterns of Spode, or kinds of automobile tires; most of us have been led into some level of specialization with superior knowledge resulting.

At first what we learn about anything is usually second hand, obtained from a book or a friend, and accumulations of such bits of information are as far as we usually go. But not always. A passion for more

can develop, and a lot of second-hand learning evolving into much personal observation can result in the object itself becoming one's most important source of information. The observer has then learned to read the object. There is in this evolution the ultimate graduation from depending on doubtful authority to consulting the object itself about itself. This is the essence of science, going to the source, and seeing or otherwise sensing what others too can verify if they wish to do so.

In museum staffs there can be much the same range of observational habit. To some a nail is a nail with little additional detail noted; to others the beginnings of classification result in awareness of some nails being square and others round; a few might be able to translate what one nail is "saying" into a half-hour story beginning with the decade when it was made. To this last person a nail is a cluster of known facts that he has trained himself to see in the nail itself, and to know what they mean. In our culture the people best able to do this accurately with the widest range of objects are the best of the curators and technicians working with museum collections.

The other extreme from the trained eye reading the nail's message is the eye hardly in focus and not pausing to examine it. This eye may be connected to a nimble enough brain that registers the nail's presence and uses it to intellectual advantage, but here the mind is most apt to go *out* from the nail rather than *in* to it, if it goes anywhere. It may be a clue, for instance, that a building once stood nearby, and that a few bones found are probably those of a domestic animal, and that the open glade nearby is probably the last remnant of a former cluster of fields. The inquiring mind, in short, can go "object-out" or "object-in" when encountering an object. The former is the more common, and strangely can be the dominant one even in museums. This I find both ironic and disturbing (Edwards 1980).

The foundation of any museum is a collection of things — usually tangible things — assembled for safekeeping, study, public exhibition or other public exposure. In museums such things are quite out of any meaningful context, their museum environments giving no information about their former lives or their former times in previous environments. One might expect therefore that in museums there might be some emphasis on considering the object for what it alone reveals, object-in. Instead, in the museum's exhibition halls when presumably viewing some of the museum's choicest treasures, the helpful labels or the well informed guides usually use the object as simply an illustration for a story about another time in another place, a story not really about the object at all. The mind is taken far afield. Rarely is one encouraged to look hard for meaningful detail held by the object itself. The object-in approach can in fact be a rare and quite memorable event when it seems logical that all those interesting things so lovingly cared for in museums would be the very centres of attention in themselves.

Behind the scenes in museum workrooms and laboratories the object is more often under close scrutiny, but with surprising frequency the data on file about objects are entirely object-out. The object held with almost no intrinsic understanding is by no means found only in the tiny village museum. In all kinds of museums the files on objects can be dominated by brief biographies of donors and histories gathered from donors' families about objects' pasts, accounts certain to be short on facts while long on family myth, half-remembered misinformation, and the doubtful tales of the aged. The family antique brought around the Horn by sail from Hamburg five generations ago can in fact be made in Japan in the 1930s.

Unlike most history, that supplied by historic objects themselves is verifiable. Objects are tangible bits of the past reaching forward into our time, so they are accessible history to be enjoyed, studied, tested, and puzzled over. The old object is a record of its past, information on both its own origins and on at least some of its adventures during its journey through time. In contrast, spoken and written history is hearsay, suspect of accuracy, sure to be shaped considerably by one or more of human bias, limitations of descriptive powers, falsehood, censorship, and unreliable memory. Hearing the changing stories from an aged parent can reveal the dangers unavoidable in collecting history from old minds; hearing two young witnesses describe the same small event can be equally revealing.

Object-in information can be found at several levels of seeing. Just seeing what most people can see, but understanding from it what most people are unable to translate, is a level of skill available to everyone with useful sensory equipment. Recent studies of Northwest Indian ceremonial and totemic objects, currently celebrated as high art, have produced understandings now available to everyone on the styles produced by different cultures, and on the rules governing to some extent their colours, shapes and surface designs (Holm 1965). With some knowledge one's reaction to this art changes from bewilderment at objects both meaningless and seemingly grotesque to a growing enjoyment of its meaning, and pleasure from artistic skills. Inspiring experiences can result from appreciation of design excellence, ingenuity in composition, quality of workmanship, and sometimes even a hint in the detail of who made the object in the dim past.

Equally evident on any object can be the evidence of its experiences, wear from use, evidence of repair, fading from age, scars from abuse or neglect. These are part of both man-made objects and those "natural" specimens taken from nature.

Sophisticated modern aids can extend the senses beyond their normal perception. Magnifications, energy wave penetrations, and chemical analyses offer a host of technological extensions of our senses that can reveal unexpected, otherwise hidden, information that the object holds. The obsidian used as weapon points by Indians can reveal its own geographic sources, for each flow of this volcanic glass has its own chemical composition (Nelson 1976). The kinds of wood in artifacts are identifiable to species under magnification, which reveals small stories of carver's choices, or trade routes to wood sources, sometimes of the possible age of the artifact. Chemistry can aid in dating rock and organic materials. The chemistry of feathers can suggest the geographic origins of waterfowl.

Recent studies at the British Columbia Provincial Museum have revealed an exciting potential for objects to hold unexpected information (Loy 1983). Archeological collections from stone-age sites in some parts of British Columbia yield artifact collections rich in micro-blades, sharp little stone knives less than 10 mm long. These were a mystery — how were they used? — until the waterlogged Ozette site in the State of Washington revealed one of the blades bound into the split end of a small stick to make a scalpel sharper than a modern steel one. Evident marks of use on Canadian examples of these blades led Loy to discover that the marks were blood residues intact after thousands of years in the soil, and then led him to methods for identifying the blood to the species of animals that the blades once cut. A new window has begun to open on the potential value of stone-age tools, providing a new view into the past. Phrases like "objects are information," and "museums are information banks" take on the role of obvious statements no longer bordering on being unnecessarily dramatic when a 10,000-year-old knife may hold information on both Ice Age man and the Ice Age fauna that sustained him.

For several reasons this discussion has avoided reference to biological collections when other examples could be found. Museums have many kinds of collections, among which biological collections hold objects less unique than most biologists believe. Museum collections of all kinds share common purposes and problems as well as possessing features to some extent unique, but differences can become magnified in practice. Some are real and major, as has already been emphasized, but there is much to be gained by appropriate stressing of their similarities. Many apparent differences in curatorial philosophy among historians, anthropologists, biologists, and even subdivisions within these disciplines, are traditional, reflecting historic accident more than inherently different needs. More collections of historic artifacts, for instance, need more of the study and research commonly focused on biological collections; and the reverent care often associated with the curation of historic (especially ethnographic) artifacts would prolong the lives of biological specimens in some museums.

Obvious differences do exist between biological specimens and the artifacts of history and anthropology. Most evident are their different origins, specimens being mostly entire organisms, their parts, or sometimes examples of structures they have made, all quite distinct from artifacts, which are man-made objects by definition.

Museums make a distinction between "specimens" and "artifacts" but, strangely, most biological specimens are thoroughly modified by man so are all really artifacts too. Their man-induced transformations are often considerable. Botany collections are dominated by plants squashed flat, then dried like misshapen hay. Most birds and mammals in collections are simply leather pillows, fresh hide stuffed with cotton, then dried. Mushrooms, snakes, frogs, fish, the huge array of soft-bodied invertebrates, and others including species more often dried, are preserved in strong fluids that can discolour and distort tissues. Most biological specimens are in fact manufactured, or heavily modified, so strictly speaking are artifacts.

The wonder is that traditional biological specimens are as useful for scientific research as they are, there is so little left unmodified (Edwards 1979a). While some are more complete than they appear, few would win any beauty contest, even those renowned for good looks when alive and well. Hence, the curator in biology is severely handicapped as a communicator with the public when compared with his colleagues in history and anthropology, who can have predominantly pleasant to beautiful-looking objects that move handsomely from the field to the museum, then from the storage shelf to the display case. A biology curator is in fact lucky to have any specimen not more or less meaningless or even repulsive in the eyes of the lay public, or to his colleagues in other disciplines for that matter. Preservation methods for biological specimens seem to be stuck in the last century (Edwards 1979a). Freeze-drying is a

noteworthy exception. Still, there has been small effort to solve the complex problem of preserving life-like biological specimens that truly resemble what they are meant to represent. For both curators and their audiences, more realistic biological specimens would be objects much more valuable as information.

Another difference between the biology-specimen and the history-artifact dichotomy of collections in museums is said to be the great advantage, in collections management, of the fact of the species and the help of the Linnaean classification that can be used to organize biological collections meaningfully. Thus the objects go naturally into clumps (50 robins), robins go with other thrushes (nine species), and in addition, more robins ("a robin is a robin; they're all the same") are always available to the collector. However, useful generic and specific clumpings occur in all collections, while the unique replaceability of the biological specimen is a myth.

Both organisms and artifacts have useful existing classifications. The species and their various clumpings of related species do give an internationally recognized system for imposing some order on biological collections, but the species is not a population of identical organisms, individuals and populations of individuals within species being somewhat different from one another. This variation is the central academic concern of many curators in biology. Since one robin in the collection does not truly represent all robins, it is a real problem to know when a collection has enough robins. Similarly, each robin being somewhat unique (just as you and I are unique) a destroyed specimen is not replaceable. The loss of a biological specimen can be just as serious as that of an historic artifact.

The human history disciplines of museums have a "species" concept as useful as has biology. Tables, for example, are a genus of furniture. Most tables, like most thrushes, are identifiable at a glance. There is perhaps more variation in the details of tables than of thrushes, in fact a seemingly infinite combination of variations seems to exist within the constraints demanded for an object to be a table. But this variability is somewhat misleading. The tables most successful through history, aesthetically and functionally, have survived by being endlessly copied. Survival of the fittest has resulted in successive generations of many recognizable lines of tables, while outside these viable "species" are the misfits, not successful perhaps but slow to be eliminated.

The successful lines, like Jacobean, Louis XV, Queen Anne, Sheraton and Victorian are those most collected and studied in museums. About these classic lineages is a swarm of misfits not unlike the constantly produced "inferiors" in the biological theory. The living misfits are more quickly recycled, however, so do not survive to clutter their habitats, or collections.

This concept of artifacts is not far from the fine art museum's emphasis on the finest of traditional design and workmanship, but to be useful in the museum of history it must use the idea at all levels of taste and affluence in order to include consideration of all populations of tables. The poor people and those not so poor are also part of history, and they presumably had their own successful and viable lineages of artifacts.

This somewhat fanciful digression into "species" of tables is not so far from the research of biological collections as at first appears. Biology has lessons to teach its sibling disciplines in museums, and one is that the basic study, therefore the research essential to other research, is that establishing meaningful classifications. The task is seldom easy, and worse is often unacknowledged as necessary. This myopia in the museum somehow ignores the simple fact that if you cannot recognize and identify the "species," you cannot do much else with it that is meaningful to others. Classifications made usefully accurate by scholarly study are the foundation of knowledge about objects. This applies to robins no more than to jade arrowheads, Kwakiutl soul catchers, or mustache cups. Work on evolving useful classifications is therefore at the very foundations of what museums exist to do, and the task in many areas is hardly begun.

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2. BOTANICAL COLLECTIONS IN MUSEUMS

R.T. OGILVIE

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Thereupon,...dispersing into gardens, meadows, fields, and mountains, they plucked whatever they found growing there and piled it into such heaps that many years would scarcely suffice for its mere sorting and scanning. Then each snatched from the heap what he saw fit or happened to lay his hand on and running to the ripped-up body, measured it with the limbs as to their length, width, and thickness. One said that it fitted; another denied it. Then they shouted at each other in dispute; they had great controversies about the very names of the herbs.

— John Amos Comenius (1663)

I. INTRODUCTION AND HISTORICAL BACKGROUND

Museum collections of plants are the basic materials for much of botany. They are the ultimate reference for the identification of unknown plants, they are the foundation for botanical nomenclature and taxonomy, they are the bases of all floras and taxonomic monographs, they are a historical archive for diverse botanical studies, and they are a source of materials for education and public information.

The term herbarium for museum collections of plants has long-established usage by botanists, and will be used in the subsequent discussion. Also, this chapter will focus primarily on herbaria of dried pressed plants, and will not deal specifically with other forms of plant collections such as fossil plants (see Chapter 8), the live collections in botanical gardens and arboreta (see Chapter 15), or live bacterial type collections. Smith (1965) has discussed the special preservation methods for specimens of algae and fungi using microscope slide mounts, dried sections, and vials with preservative fluids.

Although definitions tend to be inadequate they do have the virtue of providing a single succinct statement and revealing various points of view on the subject. Two definitions which are concise and informative, are: the herbarium is *a collection of dried plants for educational and research purposes*, and a *special kind of museum, a reference source and data bank, for past, present, and future studies in botany* (paraphrased from Radford *et al.* 1974:751).

Modern herbaria now contain not only the preserved plant specimens, but all the supporting documentation for the specimens: accession catalogues, collectors' field notes, journals and logs of col-

lecting expeditions, files of correspondence on collections, check-lists of collections, distribution maps, files on loans and exchange of specimens; as well as diverse accessory collections: seed collections, pollen collections, wood collections, microscope slides of organs and chromosomes, chromatographic strips, and electron micrographs.

The herbarium dates back to Renaissance Italy, where it was originated by Luco Ghini around 1515. The assembling of dried pressed plant specimens was continued by Ghini's students and was rapidly adopted by all European botanists (Stearn 1957). These earliest herbaria had the sheets of dried plant specimens bound into volumes, a practice which continued into the eighteenth century when, through the influence of Linnaeus, the sheets were kept separate to facilitate sorting and re-arranging the specimens.

Herbarium collections from throughout the entire history of plant taxonomy are still in existence. The oldest existing herbarium, dating from 1523, was contemporaneous with Caesalpino, who is considered to be the first plant taxonomist. Other examples of historically important herbaria are those of Bauhin (1560-1624) who introduced binary nomenclature; Tournefort (1656-1708), the originator of a modern concept of the genus; and from the eighteenth century, Linnaeus's herbarium which is the basis for the starting point of botanical nomenclature; and the herbaria of the de Jussieu and de Candolle, the formulators of a modern concept of plant families (Lawrence 1951).

II. FUNCTIONS OF HERBARIA

A. Repositories for Type Specimens and Important Historical Collections

The herbarium is an archive for type specimens and historical collections. In this function it is the cornerstone of plant nomenclature and taxonomy. The International Code of Botanical Nomenclature (Stafleu 1978:3, 6-7) states: "The application of names of taxonomic groups is determined by means of nomenclatural types" (Principle II), and "The application of the names of taxa of the rank of family or below is determined by means of nomenclatural types" (Article 7). The nomenclatural type of a species, subspecies, variety, or form, is a herbarium specimen. The name of the taxon is permanently applied to the type specimen. The type specimen, together with the published description, forms the basis for formulating the concept of the taxon to which a name is to be applied (Jeffrey 1982). Foremost among collections of type specimens is the Herbarium of the Linnaean Society of London which contains most of the original specimens of Linnaeus (13,800 specimens), which are the ultimate authority for Linnaeus's "Species Plantarum," the starting point of botanical nomenclature (Stearn 1957). Other herbaria with large numbers of type specimens are Kew with 300,000 type specimens out of a total of 5 million specimens; the New York Botanical Garden, with 73,000 type specimens out of a total of 4.3 million specimens; and Leningrad with an unspecified large number of types, in their total collection of 6 million specimens (Kent 1957).

Besides type specimens, the original collections from newly explored regions are valuable reference collections of the first records of the plants of the area. Important eighteenth century collections from the British Columbia coast are the Haenke specimens of the Malaspina Expedition at Prague, the Mocino specimens of the Quadra Expedition at Madrid, and the Menzies specimens from the Vancouver Expedition at the British Museum and at Edinburgh. The collections of Drummond and Richardson from the Franklin Arctic expeditions are at the British Museum and Kew, and the Bourgeau collections of the Palliser Expedition from the Rocky Mountains and Prairies are at Edinburgh and the Gray Herbarium. Many important early collections from western and Arctic Canada of Macoun, Malte, and Porsild are at the National Museum and the Biosystematics Research Institute in Ottawa. Rollins (1965:116) has commented on the value of historic specimens such as these: "What a satisfaction it is not only to read the account of the botanical explorer and discoverer, but also to have in hand the objects, the specimens, about which he wrote. We do not have to be satisfied with the written page. We can check the specimens to see if the plant was what he said it was and whether he was accurate or inaccurate in his observations."

B. Research For Taxonomic Monographs and Floras

Fosberg and Sachet (1965) discuss the unique position in the sciences of biological taxonomy in having a primary source of materials for study in the form of biological specimens. This contrasts with other sciences which work with secondary sources of recorded experimental and observational data, all of

which are susceptible to incremental error in recording. For biological taxonomy "the museum affords a practical means of concentrating in one place and in convenient form for study primary materials from over the entire earth. The concentration of (specimens) from many places and its subsequent preservation frees the science, in a large measure, from the tyranny of words and errors that occur in their recording, use, and interpretation. A taxonomic work that is based upon a properly collected and preserved series of specimens need not depend for its entire value upon the words in which it is expressed or the conclusions drawn by its author. The specimens which are its foundation will last indefinitely and may always be examined" (Fosberg and Sachet 1965:17).

The effectiveness of herbaria for research lies in the fact that they contain a vast sampling of the plant taxa for research in the preparation of floras and monographs. "The characters most used in taxonomy are those that are relatively easy to preserve and observe. Taxonomists have worked largely in museums, using specimens collected by generations of their predecessors as well as by themselves. They have been able to work to some extent with statistical samples of the natural populations. The samples available to taxonomists in museums provide much more information than the individual taxonomist could gather for himself" (Cronquist 1964:8). "There is no effective substitute for the herbarium in determining the geographic and morphological limits of a species. No one person can hope to see in the field any large number of species, in each of its various guises and throughout its geographic range, but in the herbarium these very things can quickly be done for many species. In the herbarium one can travel from Maine to Alaska and California and back again in five minutes" (Cronquist 1968:181).

Some concrete examples are instructive. Argus's monograph (1973) of the willows of Alaska and the Yukon, covering 41 species and 20 subspecies and varieties, was based on the study of 3,000 of his own specimens, plus examination of specimens from 13 other herbaria. Douglas's monograph (1982) of the 350 species of the Asteraceae of British Columbia involved examination of approximately 50,000 specimens in 9 herbaria. Henry's (1915) "Flora of Southern British Columbia" was based primarily on his own private herbarium of probably less than 5,000 specimens which unfortunately were destroyed through negligence (Boivin 1980). Eastham's (1947) "Supplement to the Flora of Southern British Columbia" was based on the collections at the British Columbia Provincial Museum and the University of British Columbia, as well as the agricultural herbaria at Vancouver and Kamloops; perhaps a total of 20,000 specimens in all. Carter and Newcombe's (1921) "Catalogue of the Flora of Queen Charlotte and Vancouver Islands" was based primarily on Macoun's and Newcombe's collections of about 6,000 specimens, now at the British Columbia Provincial Museum. Among modern floras, Calder and Taylor's (1968) "Flora of the Queen Charlotte Islands," comprising 593 species and subspecific taxa, was based on more than 25,000 of their own specimens, plus examination of all other known collections at five herbaria. The comprehensive "Vascular Plants of the Pacific Northwest" (Hitchcock *et al.* 1955-1969) comprising approximately 4,000 species, was based primarily on the collections at the University of Washington and Washington State University (approximately 500,000 specimens), and secondarily on collections at 15 other herbaria.

For such floras and monographs, standardized herbarium techniques make possible the precise citation of specimens by reference to collector or accession number, and designation of the herbarium housing the specimens by an acronym (Radford *et al.* 1974; Holmgren *et al.* 1981). Herbarium techniques are also applicable to mass sampling and population studies of species variation (Anderson 1941, 1967; Benson 1962; Brenan 1968).

C. Documentation for Phytogeography

The essential requirement of herbarium collections for the study of the geographic distribution of plant taxa has been referred to in the previous section. The specimens are the documentary evidence for the occurrence of the taxa in a geographic locality. Other forms of distribution records such as sightings, field lists, or photographs, mostly are not acceptable as documentation. Many herbaria also maintain distribution maps based on their collections and those of other herbaria. For further discussion of museum collections and phytogeography, see Chapter 7.

D. Loans, Exchanges and Exsiccatae

Botanical collections are made available to other herbaria through loans, exchanges, and the issuing of exsiccatae.

The loan of specimens between herbaria is widely practiced. Through loans, a wider range of specimens is made available for taxonomic research for monographs and floras, and phytogeographic research on distribution records of taxa.

Through exchange of specimens among herbaria, duplicate collections receive wider dissemination, collections from local herbaria become deposited at national herbaria, and collections from national herbaria are made available to herbaria in the region where the specimens were collected.

Exsiccatae are sequentially numbered, duplicate sets of annotated specimens, authoritatively determined by specialists, and issued to certain herbaria. They provide a set of authoritative reference material for identification and for assuring the consistent application of plant names. The issuing of exsiccatae was a common practice in the nineteenth and early twentieth centuries, and many exsiccatae included valid descriptions of new species. Such exsiccatae are treated as formal publications since they exist in several identical sets, are serially numbered, have a designated author, and place and date of first issue (Pfister 1982). Although the issuing of vascular plant exsiccatae are now less common, it is still practised for cryptogams (Sayre 1969; Andrus and Vitt 1975, 1977, 1979).

E. Reference Collections for Identifications

A primary use of any plant collection is for determining the identity of unknown specimens. In actual practice, plants are initially identified using keys, floras, or monographs, but final confirmation is done by comparing the unknown specimen with herbarium specimens. For this purpose, reference herbaria are essential for all educational institutions teaching courses in plant taxonomy. At most universities an expendable teaching collection separate from the main research herbarium is used for classwork, to prevent wear and tear on the valuable specimens.

Small reference herbaria of local plants are often maintained by agencies such as forestry, range management, wildlife, and agriculture, for identifying common plants that they deal with.

F. Repository for Voucher Specimens

Modern herbaria serve as repositories for voucher specimens from floristic inventories carried out by various agencies (see Chapter 12). Agencies benefit by having specimens identified or confirmed by the herbarium, as well as having the specimens permanently stored there. The herbarium benefits by increasing its sampling of taxa and, in some cases, by obtaining specimens of taxa which are rare or from previously uncollected areas. Despite such mutual benefits, the current increase in floristic inventories and environmental impact studies has induced societies such as the Canadian Botanical Association and the Association of Systematics Collections to look closely at the problem of voucher specimens (Lee *et al.* 1982). For scientific validity all projects entailing floristic inventories must be based on properly preserved and publicly available voucher collections. This can put a heavy burden on the staff and facilities of herbaria to identify and store large collections of voucher specimens. The problem of obtaining high quality voucher specimens can be solved best by herbaria providing training workshops in techniques of collecting, pressing, drying, and labelling specimens.

G. Source Material and Voucher Specimens for Ancillary Research

"Herbarium specimens are now used for studies in disciplines which were probably never even dreamed of at the time early collections were made and herbaria organized" (Radford *et al.* 1974:751), such as anatomy, chemotaxonomy, cytotoxicology, genecology, electron microscopy, hybridization, palynology, and population biology (Heywood 1968a,b, 1971; Metcalfe 1968; Smith 1976; Jones and Luchsinger 1979; Stace 1980).

Voucher specimens of the plants used in such studies are essential to permit re-examination of their identity. Many of the early chromosome counts and biochemical analyses of wide-ranging and polymorphic species are of doubtful value because there are no voucher specimens to re-check their identification.

Herbarium collections can also provide the plant materials for some of these studies. With a modicum of care, and under the supervision of the curator of the collection, herbarium specimens can provide pollen, seeds, floral and vegetative materials for palynology, biochemical analyses, chromosome studies, electron microscopy, and anatomical study.

H. Source Materials for Public Exhibits

An important activity of all museums is their public exhibit and education program. Carefully conceived and imaginatively presented exhibits show the wealth of specimens held by the museum, the fascinating information to be derived from the collections, and the diversity of studies carried on by the museum staff. Such exhibits can be informative and entertaining, as well as beneficial to the museum through the public support they elicit. Exhibits based on herbarium specimens, botanical art, whole plant and micro-photographs, as well as artistically fabricated models of plants and vegetation communities, are all effective in presenting the botanical museum to the public.

III. MAJOR, REGIONAL AND LOCAL HERBARIA

The role and function of major, regional, and local herbaria have been discussed in many works (Davis and Heywood 1963; Turrill 1964a; Beaman 1965a,b; Rollins 1965; Brenan 1968; Cronquist 1968; McNeill 1968; Shetler 1969).

Major herbaria hold collections of several million specimens covering the world flora. They include many type specimens and valuable historical collections, some examples of which have been referred to above. There are perhaps 18-20 major herbaria in the world. Historical accounts of several of these major herbaria have been published (Turrill 1959; Cloukie 1964; Shetler 1967; Fletcher and Brown 1970; Stearn 1981; Walters 1981). In general, large-scale botanical works are pursued at major herbaria: revisions of classification systems, monographs of major taxonomic groups, and floras of regions and continents.

A very important function of major herbaria is the loan of specimens to smaller herbaria. The accessibility to botanists around the world of type specimens and important historical collections has been facilitated recently by the technique of microfiche. Microfiche copies are available for all the specimens of 26 historic herbaria, including those of Linnaeus, Tournefort, de Jussieu, and de Candolle.¹ The collection of 73,000 type specimens at the New York Botanical Garden Herbarium is also now available on microfiche.²

Regional herbaria contain collections of usually less than one million specimens, from their own and adjacent countries. They include many national, state, provincial, university, and museum herbaria. In addition to their collections of regional flora they serve as a repository for voucher specimens from mass collections, population and ecological studies, and diverse ancillary disciplines. The collections form the bases for a variety of botanical research and for the preparation of national and provincial floras (Turrill 1964b).

Local herbaria are small and restricted in the scope of their collections, and include reference and teaching collections. Private personal herbaria of individual collectors are usually local in scope but nevertheless may contain both rare species and comprehensive collections from certain areas. Most private herbaria contain only a few thousand specimens, although some private herbaria in Canada contain up to 40 thousand specimens (Boivin 1980). Local and private herbaria are vulnerable to short-term planning and curation, neglect, and deterioration. Reference herbaria may be abandoned with a change in the project or staff for which the collection was made. At the time when these herbaria are being initiated and assembled some forethought should be given to how long they can be maintained, their long-term curation, and the possibility of eventually incorporating them into regional herbaria when they can no longer be housed and curated locally.

1. Inter Documentation Company, Zug, Switzerland

2. Meckler Publishing Company, Westport, Connecticut

IV. HERBARIUM LITERATURE

A number of catalogues and indexes of herbaria have been published. Most important of these is "Index Herbariorum" which contains details of all the herbaria of the world (Holmgren *et al.* 1981) and a summary of all the collectors (Lanjouw and Stafleu 1954, 1957; Chaudri *et al.* 1972; Vegter 1978, 1983). A detailed survey of Canadian herbaria has been prepared by Boivin (1980), and periodic listings and summaries have been done by the Canadian Botanical Association (Woodland 1979).

Recently there has been closer contact and exchange of information among regional herbaria. The Pacific Northwest Herbarium Consortium of 16 herbaria holds irregular meetings and issues an informative newsletter (Scagel 1976-1984). A similar consortium of 46 California herbaria has been recently formed, and produces a newsletter (Duncan 1980-1984). A newsletter covering the activities of North American herbaria was initiated in 1981 by the Missouri Botanical Garden (Morin and Crosby 1981-1984).

Herbarium techniques and procedures have been abundantly discussed in the literature, and only a selection needs to be listed here: Savile (1962), Fosberg and Sachet (1965), Leehouts (1968), Smith (1971), Brayshaw (1973), Croat (1978), Hicks and Hicks (1978) and Faber (1983). Some recent techniques for herbarium fumigation using freezing and microwave have been reported (Cowan 1980; Hall 1981; Hill 1983). Valuable summaries of herbarium ethics and practices have been compiled by Kobulski *et al.* (1958) and Nevling (1973). A revealing analysis of the costs of herbarium services has been prepared by the American Society of Plant Taxonomists (1979).

V. LIMITATIONS OF BOTANICAL COLLECTIONS

Standard techniques of preparing botanical specimens are effective in preserving salient taxonomic features, but limitations of herbarium specimens have long been recognised. Certain structural features are poorly preserved; these include succulence, surface-textural features, and three-dimensional branching and shape. Some colour features are lost with drying, such as floral colour, glaucous surfaces, and the pigmentation of non-chlorophyllous plants (e.g. some Orchidaceae, Monotropaceae, Orobanchaceae).

The wide phenological and phenotypic variation which some plants undergo during their life cannot be recorded by a single specimen (Cook 1968). Repeated sampling of different stages of a plant are necessary to show this variation (see Chapter 13).

Inadequate collection data attached to specimens are a serious limitation to some herbarium material. Mostly there is no way of rectifying this deficiency unless additional information on the specimen can be gleaned from the field notes of the collector. One of the contributing factors to inadequate collection data is the small size and poor design of many herbarium labels.

Incomplete collection data can severely reduce the value of herbarium specimens for phytogeographic information. For ecological information herbarium collections are even more limited. It is not possible to derive meaningful ecological information from the labels of most herbarium specimens.

A limitation of herbarium collections which is recognised by all taxonomists is the erroneous identification of some of the specimens. The important point here is that all users of the collections, including non-taxonomists, are aware that some of the plant names on the labels are incorrect and that the identification cannot be used uncritically.

There are a number of ways in which the research value of botanical specimens can be increased. The quality of the specimen itself can be improved by the careful practise of standard collection techniques: collecting all parts of the plant — flowers, fruits, underground parts and bark; and recording on the specimen label those features not present or poorly preserved in the specimen: colour, growth form and, for woody plants, height, diameter, and branching habit. In general, much more information should be recorded on the specimen label; there needs to be more details on habitat features, associated vegetation, relative abundance, and range of variability of the species.

We now know a great deal about population structure and ecotypic variation of plant species, and this knowledge should be reflected to a far greater degree in how herbarium specimens are collected. There is need for much more intensive sampling of plant species over their geographic and ecological range to represent the population, ecological, and geographic variation in their morphology (Valentine 1978).

A diversification in the kinds of specimens is another direction in which herbarium collections can be improved. Specimens of seeds, pollen, wood, anatomical and cytological slides, and ethnobotanical materials greatly enhance the value of botanical collections. The cataloguing and storing of such materials require curatorial flexibility in established herbarium procedures. Although such specimens have to be accommodated separately from conventional herbarium sheets, they require the same procedures of cataloguing and accessioning in addition to cross-referencing with the rest of the herbarium collection.

VI. CURRENT TRENDS IN HERBARIA

Twenty years ago, forecasts on the trends in systematics and biological collections for the "foreseeable future" (approximately 10 years) were presented by Sokal (1964:43-44): "What will the museum of the future look like? It will consist of preserved specimens, but these will be preserved in various ways depending upon the purpose for which they are needed. Since the characters necessary for an analysis of systematic affinities and for identification will be not only those superficially visible on conventionally prepared specimens, the specimens will need to be prepared so as to permit such study. The present-day type specimens, hoarded as treasured possessions of the museum's curators, are more likely to become demonstration specimens to be replaced by others when the occasion calls for it. Also it may not be necessary to maintain preserved collections of all species in order to give the student of nature an idea of organic diversity. Possibly some landmarks showing the variety and form of the organic world may be sufficient. The role of the type specimen both as the name bearer and as a 'repository' for characters is likely to be taken over by one of various devices for recording a multitude of characters. If the trend of taxonomy is in a chemical direction, it may very well be that permanently prepared paper chromatogram strips or electrophoretic records will be kept as records of the species. More likely, however, is some storage of these in electronic form on spools of magnetic tape or in some other way accessible for computer processing. This would permit the mixing of morphological and other data with biochemical results. These records could be gone through whenever an unknown form would have to be compared with known ones. They could be used for identification purposes and could also in general provide summaries of the variation encountered in different groups of animals and plants." Although his forecasts have not been realised, perhaps his criticisms of "the conservatism and stagnation" of museums and taxonomy did provide a stimulus for the innovations that have taken place.

There has been a major advent in the use of computers in herbarium collections (Brenan *et al.* 1975; Pankhurst 1975; Faber 1983). There has been computerisation of the data of type-specimen collections (Shetler 1973), of herbarium labels (Argus and Sheard 1972; Gillett 1983), and of distribution maps (Soper 1964, 1975; McAllister 1983). Computerisation of collection data is available (Brenan *et al.* 1975; Wetmore 1979; Pinder-Moss 1983), although the questions of "what to record" and "how much to record" remain unresolved (Perring 1975). Computer programs have been designed for the construction of taxonomic keys (Pankhurst 1975; Ceska and Trumpour 1979; Beaman *et al.* 1980) and for the identification of specimens (Pankhurst 1975; Beaman *et al.* 1980). Another important advance has been the increased accessibility to type specimens and historical collections through microfiche.

This is yet another aspect of the fruitful exchange of information and healthy cooperation among world herbaria. The comments of Fosberg and Sachet (1967:105) of almost 20 years ago are just as true today: "Since science knows no boundaries, it seems proper to regard herbaria not as strictly national properties, but as assets of the entire botanical world. Their welfare is of general botanical interest. As long as active contacts are maintained between the herbaria of different countries, systematic botany and plant geography will continue to thrive."

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3. THE SIGNIFICANCE OF TYPE SPECIMENS AND OLD COLLECTIONS TO RESEARCH IN THE BIOLOGICAL SCIENCES

W.B.N. BERRY

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I. INTRODUCTION

Museums and libraries have many similarities. Both are archival in activity and, accordingly, both may be viewed as having comparable use, storage, and data-retrieval operations. Both libraries and natural history museums house stores of data that may be drawn upon for a broad spectrum of studies. As natural history collections and book collections grow and research programs that draw upon them change over the years, sections of the collections may lie dormant for long periods of time. Then, suddenly, they will have a vital use. Certain collections of birds' eggs, for example, lay untouched for years until a need arose to examine eggshell thicknesses to evaluate the potential effects of the use of DDT on bird reproduction. Then, collections of birds' eggs in museums that had appropriate collection information were sought and used in a study of considerable significance to mankind.

Old and type collections in natural history museums may be likened to materials in libraries that have extensive collections of old books and periodicals as well as a substantial rare book component. The type collections are, as are rare books, part of man's cultural heritage. Type collections must bear the same relationship to a museum's operations as rare books do to a library's, as indicated in Article 72 of the "International Code of Zoological Nomenclature" which states: "Types are to be regarded as the property of science by all zoologists and persons responsible for their safe-keeping." Type collections are indeed not simply the property of a single institution; they are the fundamental materials that underlie the entire domain that is organismal biology. They are the cornerstones upon which man's understanding of organismal relationships and distributions are built. Accordingly, collections of type specimens or rare books should be treated alike. Both need to be handled with concern for their conservation and safety. Both should be used judiciously.

The old collections in natural history museums have been used by scholars in a manner similar to those many shelves of volumes, many from an age long past, that grace the walls of libraries in many parts of the world. They, too, are a part of mankind's heritage for they record data no longer obtainable in many instances and they provide an enormous trove of data that awaits the imaginative inquisitiveness of generations of scholars to come. Old collections bear the same relationship to natural history museums that books do to a library. They are the reason for its existence and the trove of informational treasure they house awaits to kindle the imaginations of the inquisitive for generations to come. These collections encompass a vast store of information relevant to distributions of organisms as well as relationships among organisms. They constitute the data base for studies in biogeography, evolutionary biology, ecology, and systematic biology. These collections are similar to the older books and periodicals in libraries in that they are a rich and valued resource for scholars and an anathema to administrators charged with holding down costs and providing space for the less prosaic or more "modern" tools of research. To the former group, museum collections are a storehouse of data waiting to be evaluated and used. To the latter, the same collections are seemingly useless drawers and boxes of old bones, shells, leaves, and rocks that could be easily cast aside to make room for the equipment and the personnel associated with it that suggest "advanced" or "high-powered" research.

Despite their mundane aspect, natural history museum collections are as basic to research in organismal biology as compounds are to a chemist. They provide the data basic to many existing hypotheses on organismal relationships and distributions. They provide the data that may be used by later investigators to rerun any experiment involving organismal identities, relationships, and distributions. They provide information relevant to appropriate use of certain lands, and they provide a baseline for assessing man's impacts on the natural environments in which he lives. They contain information relevant to understanding the forces that shape change in organisms and organismal associations through time. For an experimental scientist, they provide the data that permit an original experiment to be re-evaluated and its conclusions re-examined. Museum collections are a part of the ingredients basic to scientific research in biology.

II. A HISTORICAL PERSPECTIVE

Natural history collections have their roots in the dawn of man's interest in life about him. Both Pliny in his "Natural History" and Aristotle in his "History of Animals" drew attention to the diversity of life about them. These and other summaries of organisms and their occurrences drew note from natural historians during that rekindling of interest in natural phenomena embodied in the Renaissance. As Rudwick (1976) has pointed out, the Swiss natural historian Conrad Gesner, in the mid-1500s, attempted to bring up to date the knowledge of animals. He (Gesnerus 1565) included fossils as well in his publications. In his work, he attempted to lay foundations upon which future natural historians might build, for he tried to enhance the flow of correspondence among scholars concerning the identity and distribution of animals. One of the earliest references to the beginnings of natural history museums may be found in Gesner's "On Fossil Objects," for in that work he cited the natural history collections assembled by his friend Johann Kentmann. Kentmann's collections, it was noted, were housed in neatly labelled drawers of a specially made cabinet. Gesner appears to have had the basics of museum curation in mind for he drew attention to the need for keeping appropriate locality information with the materials as well as for housing them with concern for their conservation.

Through his writings, both in book form and in correspondence, Gesner stimulated interest in natural history and in obtaining collections of the phenomena of natural history. Gradually, collections of nature's handiwork — animals, plants, fossils, and rocks — came to be recognized as valuable in documenting both the diversity and distribution patterns of organisms. Over the three centuries after Gesner's day, natural history collections grew to considerable size under several stimuli. Among them were the wonderment of a Creator's munificence, a curiosity in natural phenomena, a need for surveys of organismal distributions for economic pursuits, and a need to identify organisms in such a manner that descriptions of them could be written and sent to a correspondent. Many wealthy persons developed their own "cabinets" of natural history materials. Commonly, these included a spectrum of remains of modern organisms as well as fossils and rocks or minerals. As years passed and governments grew, diverse governmental agencies came to house collections of organisms. From the activities of both private and public organizations collecting and housing natural history materials, the collections grew apace with cultural growth and development. The collections, indeed, reflect a growth in man's interest in his ancestry and in those naturally occurring objects with which he came into contact. As private collections grew, certain of them became a part of a nation's cultural heritage for some came to be nuclei for national, city, or regional museums. The British Museum of Natural History, for example, has at the nucleus of its collections the private collection of Hans Sloane, a renowned physician. Sloane spent vast sums amassing a great natural history collection which he willed to the nation in 1753. Sloane wished that his materials might be used to enhance knowledge and to slake the thirst of the curious for information about organisms. In the materials that came to the large national, city, or other institutional collections were specimens considered typical of particular organismal species, and even included rocks and minerals. These materials comprise the foundations of the type collections. Natural history collections have a long history. That history parallels growth in scholarly and even cultural development.

III. TYPE COLLECTIONS

Of the collections that natural history museums house, those most vital to the biological sciences are the type and voucher specimen collections. These are reference points crucial to all studies of organismal identity and diversity. Type and voucher specimens contain data that are necessary for documenting and communicating about distribution patterns of organisms. Type specimens are particularly important in this regard, and permit investigators to examine data upon which other investigators' conclusions were based and, from them, to form independent opinions. Newly found specimens must often be compared with type materials to ascertain identities and to test hypotheses concerning not only identity but also relationships. Type materials are basic to the formulation of hypotheses concerning the heritage and diversity of life through time.

Conservation of type specimens is of great concern to biologists, so matters of storing and handling types have been discussed by many authors (e.g. Swinton 1955; Owen 1964). Furthermore, Recommendation 72D of the "International Code of Zoological Nomenclature" summarizes institutional responsibilities regarding type specimens as follows:

"Every institution in which types are deposited should

- (1) ensure that all are clearly marked so that they will be unmistakably recognized;
- (2) take all necessary steps for their safe preservation;
- (3) make them accessible for study;
- (4) publish lists of type material in its possession or custody; and
- (5) so far as is possible, communicate information concerning types when requested by zoologists."

The "International Code of Botanical Nomenclature" is less specific in discussing type specimens, but Recommendation 7A states: "It is strongly recommended that the material on which the name of a taxon is based, especially the holotype, be deposited in a permanent, responsible institution and that it be scrupulously conserved."

Many studies in systematic biology must draw directly upon type specimens. So too must many investigations into patterns in diversity and relationships of organisms. Systematists particularly, but most biogeographers and other evolutionary biologists as well, must use type collections in their studies because these collections include materials that are as basic to these researches as elements and compounds are to a chemist, or diverse atomic and subatomic particles are to certain physicists. The type collections link any investigator to original meanings and concepts of organismal identity. Because they do, they are the fundamental "stuff" of biology.

IV. OLD COLLECTIONS

Museums and libraries house materials that have accumulated over the years from many sources. In some instances, as has been suggested, these materials provide the basic data upon which many biological investigations are built. They comprise a part of man's heritage. They are guides to change through time, and they may be used to suggest potential future development.

Old collections housed in natural history museums or related institutions have resulted from a variety of sources, including donations, chance collecting, research programs of a number of kinds, and from surveys and other forms of assessment of resources. Those that have appropriate locality and other data relevant to their occurrence are valuable research resources.

Among the most useful of old collections housed in museums may be numbered the materials assembled in the course of wildlife surveys. Many of these collections were made by personnel of state or federal agencies in support of certain agriculture or wildlife management programs. The Fish and Wildlife Service of the United States government, for example, traces its beginnings to about 1885 when a Section of Economic Ornithology was established by Congress in the Department of Agriculture. That unit's initial goals were to obtain data pertinent to the food habits and migration patterns of birds in relation to insects and plants. A year later, under the leadership of the naturalist C. Hart Merriam, the unit expanded its responsibilities to include surveys of mammals. Accordingly, the unit became the Division of Economic Ornithology and Mammalogy with the goals of providing an expanding farming industry with information on a broad spectrum of pests and potential pests. Because Merriam was interested in the factors that control the distributions of animals and plants, the work of the unit became that of surveying animals and plants area by area. From those data life-zone maps were constructed. The survey work continued and ex-

panded over the years. As it did, the collections made during the surveys were assembled and appropriate measures taken to conserve them, for they had provided the data upon which many life-zone maps and other distribution patterns were founded. Any investigator can use the collections and associated data for similar research, or to inquire into the validity of the original conclusions.

Another example of the pattern of growth of old natural history collections concerns those at the University of California at Berkeley. When C. Hart Merriam came to Berkeley to head the Museum of Vertebrate Zoology, he brought with him his strong desire to survey animals in a number of areas and to assemble the collections made in the course of these surveys in the museum. These zoological collections joined those of botanical and geological materials given to the University by the State Legislature when Berkeley's doors opened. The materials had been stored in legislative chambers since the mid-1860s when they had been obtained in the course of geological surveys of the state. Legislators considered the materials valuable enough to conserve them, and the Legislature funded a University Museum at Berkeley during the last quarter of the nineteenth century to house the state's natural history collections. About the turn of the century, these collections began to be divided into component units, as money, much from private donors, became available to expand museum conservation as well as teaching and research based upon the collections. During the twentieth century, collections have continued to grow, primarily from survey and similar research activities, and to be used in a spectrum of systematic, ecologic, and biogeographic research and teaching programs. Today, collectively, they constitute one of the richest teaching and research resources housed at any university. They form a magnet that draws scholars from all parts of the world. Such visits enrich teaching, for the visitors come not only to study materials but also to interact with faculty and students and, immeasurably, though perhaps imperceptibly to administrators, augment teaching. In these interactions with visitors, the old collections comprise a little-recognized but valuable enrichment of teaching and research.

Many of the old collections housed in natural history museums form useful aspects of a national biological sciences heritage. These collections aid instruction, comprising a rich data base that may be drawn upon for studies in various aspects of agriculture, including range management and pest control, land use (including waste disposal), and wildlife management. They form a baseline for a number of inquiries related to issues of use and misuse of the environment, for these collections include information on organisms present and the conditions of their life prior to man's uses and abuses of a number of areas. Many collections incorporate data on the kinds of organisms that were once present in areas before urbanization. They provide clues to organismal associations in areas that have been disturbed, either by man or nature, over a period of time. They are basic to inquiries of changes in organismal associations and diversity that have taken place over the years. They may be used in evolutionary studies to examine changes in specific taxa through the years. The range of variation in morphological features may be examined using old specimens. Changes in population size, structure, and range in variation in members of the population may be assessed from the information contained in old collections. In a very real sense, old collections of organisms can incorporate the evidence of organismal morphological changes in time, thus documenting the tempo and mode of evolution. They may be used as guideposts to localities from which collections may be sought for a wide array of evolutionary biological studies. They may equally well be used as sign posts to influences of environmental change through time. Collections can be examined for diverse biogeographic and ecologic distribution patterns, and changes in these patterns. In addition to the obvious uses of old collections in systematic biology, therefore, the materials in the collections of old natural history museums document the course of evolution through not only historic but also prehistoric time.

The old collections in natural history museums await the introduction of new forms of technology that may be used in the examinations of organisms. Electron microscopy, radiography and even holography, when used in research on museum materials can lead to new insights into organismal identity and relationships. Tissues may be available for forms of biochemical assessments from materials stored in natural history museums. Studies with x-rays may reveal morphologies, structures, or, in the case of fossils, even new organisms not previously expected. Electron microscopy may reveal morphological features or anatomical relationships not expected from earlier examinations. These and comparable studies made possible by technological advances will, in turn, advance knowledge in the biological sciences if the natural history museum collections are made available for investigation. The collections await imaginative approaches to their study using current technologies as well as the technologies still to be discovered. New insights may be gleaned when old data are examined with fresh eyes and minds.

V. ON STORAGE AND AUTOMATED DATA RETRIEVAL

Storage and adequate retrieval of information from old collections becomes a problem as collections grow. So, too, do the needs of institutions that house them for other uses of the space holding those collections. A method libraries have used (and some museums as well) is to construct a large storage facility at some distance from high-use, centralized buildings. Little-used material may then be stored at some distance from the centralized research and teaching facilities. Automated data-retrieval methods now permit any museum to keep all the records pertaining to that institution's collections readily available. Comprehensive listings of a museum's holdings and the disposition of individual collections or specimens can be called to view quickly using automated data-retrieval procedures. This makes some aspects of storage straightforward, particularly those of keeping relevant data, including that of the exact place a specimen is housed.

Specimens stored at a distance from the main museum may be obtained by messenger service or may be examined at the storage facility.

Storage of data relevant to natural history museum collections using computers aids the task of collection management, and also enhances research uses of the materials. When large volumes of data are organized through computer programs, unsuspected relationships among taxa or patterns in distribution may emerge. Indeed, even effectively "lost" specimens may be "found". Organizations of data inherent in large collections to facilitate searches for unsuspected relationships is a goal of computer-assisted research using museum collections.

Development of computer-based cataloguing and curatorial procedures for natural history collections have been described by a number of authors (e.g. Rensberger and Berry 1967; Brunton 1979; Light 1979). As these and others have pointed out, collection management and the use of collections in research are both facilitated by use of computer-assisted procedures.

Museum records may be widely disseminated not only through uses of computers but also through use of fiche. Catalogues, or lists of organized data from museum catalogues, may be circulated on fiche allowing data to be circulated readily to investigators. Fiche listing permits investigators remote from museums to search for specimens pertinent to their research.

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4. MUSEUM COLLECTIONS AND THE EVOLUTIONARY STUDY OF GROWTH AND DEVELOPMENT

PERE ALBERCH

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I. INTRODUCTION

Historically, museum collections have been dominated by a typological bias, probably an offspring of traditional Linnaean taxonomy. The concept of *the type* of a species is still a cornerstone in contemporary collections. "The type" is the standard for the nominal species, the individual which represents the characteristics of the species. Two consequences immediately emerge from this perspective: (1) large series of specimens of any given species are superfluous; and (2) juveniles and embryos are substandard material since they do not possess yet a complete set of the species-specific characters. The degree to which the various museum collections adhere to this philosophy varies from institution to institution and from field to field, and has been changing through time. For example, looking back at the history of curatorial procedures in the herpetological collection at the Museum of Comparative Zoology, it was not until the mid-fifties that a policy of accessioning and cataloguing all specimens was initiated. This change in policy reflected a change in times and in scientific priorities directly related to the retirement of the curator, and his replacement by one with a different and more "populational" perspective of evolutionary biology. Prior to that time only twenty specimens (preferably adults) of any given series were catalogued; the rest were labelled as "duplicates" and used for trading with other institutions. Clearly, at that time the emphasis was on attempting to build up a collection as comprehensive as possible regarding taxonomic coverage. The idea that museum collections could be used to address problems relating to population and community ecology, as well as to gather information on reproductive cycles, had still not permeated curatorial practices. Since the importance and relevance of large series for many modern evolutionary studies are discussed in other chapters, I will not discuss these topics any further.

Current curatorial practices regarding embryonic or juvenile material are, in general, very unfortunate. I hope that this chapter helps in drawing attention to the problem. True, some individuals, due to their particular research interests, have built up very comprehensive and well curated collections of embryonic or larval material but, in general, museum curators and field collectors have had a negative attitude towards accessioning and properly curating such material. The reasons, in my experience, are twofold: (1) embryos or juveniles are considered not to be very useful in taxonomic studies; and (2) they are often difficult to identify. This is compounded by the logistic fact that embryos or larvae may require different maintenance and preservation techniques.

This review is biased by my curatorial expertise being restricted to lower vertebrates. I hope to make the information valid for all vertebrates (including fossil material), but the curation of some larval invertebrate collections may involve some qualitatively different problems not discussed in this chapter.

II. IMPORTANCE OF EMBRYONIC, LARVAL AND JUVENILE MATERIAL IN EVOLUTIONARY STUDIES

In contrast to its lowly status in museum collections, embryological material has had a central and prominent place in comparative and evolutionary morphology. As discussed in the excellent historical review by Russell (1916; reprinted 1982), embryology was extensively used by pre-Darwinian morphologists such as Goethe, Meckel, Oken, Agassiz, Serres, *etc.*, to construct a unified theory of form. These theories were modified by early evolutionary morphologists, such as Huxley, Haeckel and Gegenbaur, but still embryological evidence was not only central to their arguments, but the sole purpose of embryological work (which was mainly comparative at the time) was to obtain information about evolutionary processes. With the advent of experimental embryology, a schism appeared between developmental biology and evolution. (For reviews on this issue see discussions in Oppenheimer 1940; Mayr and Provine 1980). However, *descriptive* embryological information has remained up until today an important component of comparative anatomy, as examination of any textbook on the subject will demonstrate (*e.g.* Romer and Parsons 1977; Wake 1979). The basic idea is that to understand and analyze patterns of morphological organization one must know and understand the developmental process through which a trait develops. Recently, two new perspectives have been gaining attention in regard to the role of development in the analysis of *mechanisms* of evolutionary change. One is a renewed interest in the relationships between ontogeny and phylogeny (Gould 1977); the other is a rapprochement of experimental embryology with evolution. At various times, there have been some outstanding scientists working at this interface (*e.g.* Goldschmidt 1940 [reprinted 1982]; Schmalhausen 1949; Waddington 1957, 1975). However, only recently does there appear to be a wide consensus, among both developmental and evolutionary biologists, that integration between these two disciplines can provide some novel insights (*e.g.* see papers in Bonner, 1982). The books by Löwtrup (1974), Bonner (1982), and Raff and Kaufman (1983) are a reflection of this interest.

In this chapter, I would like to discuss the various aspects of evolutionary biology where developmental data from museum specimens can provide important information.

A. Homologies

Perhaps the most traditional use of developmental evidence has been to prove homology (or lack of it) between structures. This assumes developmental sequences to be highly conservative. That is, adult structures of different appearance and organization could be shown to be homologous if their developmental basis is similar. For example, Rosen *et al.* (1981) claim that urodele limbs are homologous to lungfish fins on the basis of similarities during some stages in their ontogeny. Conversely, traits similar in appearance can be shown to be analogous, but not homologous, by demonstrating that they form through different developmental routes.

For studies of this sort, a single embryo at the critical ontogenetic stage can be of great significance. In fact, locality data may not be critical, and properly staged and preserved material obtained from aquariums and zoos can be extremely useful.

However, the uncritical acceptance of ontogenetic similarity or dissimilarity as proof of homology can cause problems. For example, one might conclude that the spinal cord in fishes is not homologous with the spinal cord of amphibians, since in the former neurulation is by cavitation while in the latter the neural tube is formed by tissue invagination. The same problems are found when one compares early stages of development. For example, see the incisive discussion on the problem of homology among gastrulation systems in various vertebrates by Ballard (1976, 1981). The root of this problem can be found in the fact that comparative and evolutionary anatomists only use descriptive embryological information. One must go beyond description and understand developmental mechanisms to obtain a better interpretation of embryological evidence.

B. Evolutionary Polarity of Character States

A preliminary stage in any systematic analysis is to define a set of characters and their polarities (*i.e.* which state is primitive, which one is derived). Haeckel's biogenetic law, better known by its motto "ontogeny recapitulates phylogeny," offers to provide ultimate proof of character polarities. If character state A appears earlier in ontogeny than character state B, then we conclude A to be primitive. Although the biogenetic law was proven to be mechanistically untenable (*e.g.* Garstank 1928; de Beer 1930; Gould 1977), its implicit or explicit usage in establishing character polarities has been continued by systematists (review by Stevens 1980). Recently, Nelson (1978) and Nelson and Platnick (1980) have presented a revised version of the biogenetic law where, in fact, they argue that ontogenetic information is the most direct and unambiguous way to establish polarity of character states; this is a source of information which is independent from palaeontological and comparative evidence.

Paedomorphosis, inappropriately equated to neoteny in certain texts (see definitions by de Beer 1930, Gould 1977 and Alberch *et al.* 1979), poses some serious problems for this kind of analysis. Paedomorphosis is the process of achieving evolutionary change by retaining ancestral juvenile traits. Obviously, paedomorphic events would result in derived features to be identified as primitive, since they appear as intermediate stages in the ancestral ontogeny. Nelson and Platnick (1980) dismiss paedomorphosis by arguing that: (1) Terminal addition is the most common heterochronic change, therefore the biogenetic law, with a few qualifying statements, is essentially valid. Consequently it would never be a parsimonious hypothesis to argue that paedomorphosis has occurred; (2) Hypothesis of paedomorphosis usually involves loss of characters in the derived species. Accordingly, it is not proper to use lack of a character as positive information. However, their hypothesis about the untestability of paedomorphic phenomena is not correct, since the occurrence of paedomorphosis has been amply demonstrated comparatively and experimentally (see recent review by Gould 1982a). Fink (1982) has reviewed this problem and shows how outgroup comparisons can be coupled with ontogenetic information to identify paedomorphic events in phylogeny.

C. Heterochrony and Allometric Studies

Heterochrony is the evolutionary mechanism which de Beer, in an acceptance followed by most modern workers (*e.g.* Gould, 1977, 1982a), defined as: "phyletic change in the onset of timing of development, so that the appearance or rate of development of a feature in a descendant ontogeny is either accelerated or retarded relative to the appearance or rate of development of the same feature in an ancestor's ontogeny" (Gould 1977:482). Allometry is essentially a subset of heterochronic phenomena concerned with the change of shape correlated with increase or decrease in size. In allometric studies, the change in size may reflect ontogeny, phylogeny, or merely the static differences among related animals (adults of all mammals, for example).

Both of these interrelated processes appear to play an important role in evolution since they involve regulation of a developmental program. Thus, phyletic change can be achieved without altering the basic structure of the program. By a developmental program I mean a set of form-generating algorithms composed of a complex set of temporal and spatial biochemical, cellular, and tissue interactions (Alberch 1982). It is beyond the scope of this chapter to review the importance and underlying assumptions of heterochronic and allometric analysis. Good reviews of heterochrony can be found in de Beer (1930), Rensch (1959), and Gould (1977) which include historical background and relevant references. Alberch *et al.* (1979) and Gould (1982a) present updated and generalized formalisms of heterochronic analysis. The classical works by Huxley (1932) and Gould (1966) provide comprehensive reviews on allometry; Cock (1966) reviews the genetical aspects of allometric growth; while McMahon (1973) presents a functional perspective. Bonner (1965, 1974) provides a synthetic perspective of evolution and development with an ecological bent.

Museum collections are the main source of information for heterochronic and allometric analyses involving comparison among cross-sectional ontogenetic series. Unlike longitudinal data, which record the growth and shape changes of an *individual* throughout its ontogeny, "cross-sectional" data consist of a series of measurements of individuals at different ages or ontogenetic stages. Longitudinal data require live material, but cross-sectional data can be obtained from series of preserved specimens. Cross-sectional ontogenetic data lack information on individual variation in growth and development and should be

viewed as a representation of the average ontogeny for the population. For this reason it is important for museums to have large series from single localities, since mixing up specimens from various localities can result in confounding geographical variation. In Table I, I have listed some recent references of studies on allometry and/or heterochrony based mainly on museum material (the classification of some papers is somewhat arbitrary, since it is sometimes difficult to differentiate between allometric and heterochronic studies). This table does not attempt to be comprehensive. I have selected a series of references (preferably recent ones) covering a variety of topics, to illustrate the possible uses of material from museum collections. Although my selection of literature is biased by my research interests (for example, I probably ignored references on entomological studies), it points out uneven taxonomic coverage. For example, there appears to be more work on heterochrony in invertebrates and lower vertebrates than in higher vertebrates. Similarly, most of the mammal literature is on problems of differential growth (allometry) rather than differential differentiation and morphogenesis (heterochrony). I do not know if this corresponds to real biological phenomena or simply reflects tradition (*i.e.* specialists in different disciplines have focused on different problems), or methodological problems (*e.g.* difficulty of describing embryonic development *in utero*). I suspect the latter explanation to be the most likely. Nevertheless, the relative role of these various processes of growth and development in the evolution of different vertebrate and invertebrate taxa is a problem that would be interesting to survey.

TABLE I
SELECTED REFERENCES ON RECENT STUDIES ON ALLOMETRY AND HETEROCHRONY
WHICH HAVE MADE SOME USE OF MATERIAL FROM MUSEUM COLLECTIONS

HETEROCHRONY	
Mammals	
Bard (1977)	Color patterns in zebras
Birds	
Grant (1981)	Galapagos finches
James and Olson (1983)	Flightless birds
Olson (1973)	Evolution of rails
Raikow (1975)	Developmental anomalies in <i>Passerella iliaca</i> ; <i>Acridotheres tristis</i>
Raikow <i>et al.</i> (1979)	Atavistic traits in bowerbirds
Amphibians	
Alberch (1983)	Variation in <i>Bolitoglossa</i>
Alberch and Alberch (1981)	Progenesis in <i>Bolitoglossa occidentalis</i>
Hanken (1982)	Variation in <i>Thorius</i>
Hanken (1983a)	Miniaturization in <i>Thorius</i>
Larson (1979)	Paedomorphosis in <i>Aneides flavipunctatus</i>
Larson <i>et al.</i> (1981)	Role of heterochrony in the origin of morphological novelties in Plethodontini
Marlow <i>et al.</i> (1979)	<i>Batrachoseps</i> systematics
Wake (1980)	<i>Rhyacotriton</i>
Wake <i>et al.</i> (1983)	Peramorphosis in <i>Aneides lugubris</i>
Fishes	
Balon (1980)	Charrs
Balon (1981)	General; fishes
Bell (1981)	Stickleback (<i>Gasterosteus aculeatus</i>)
Fink (1981)	Tooth attachment in actinopterygian fishes
Meinke (1982)	Dermal skeleton in <i>Polypterus</i>
Weisel (1967)	Differences in the sequence of ossification between an ovoviparous species (<i>Poecilia reticulata</i>) and an oviparous one (<i>Catostomus macrocheilus</i>)

Table 1. Continued

Vertebrate Paleontology

Bolt (1977, 1979)
de Ricqlès (1975, 1980)

Gould (1974)

Roth (1984)

Paedomorphosis in the origin of Lissamphibia
Neoteny in stegocephalians and captorhinomorph
reptiles
Hypermorphosis in the "Irish Elk,"
Megaloceros giganteus
Heterochrony in elephants

Invertebrates

Gould (1969)

Gould (1972)

McNamara (1982)

Miyazaki and Mickevich (1982)

Monniot (1971)

Serban (1960)

Sprinkle and Bell (1978)

Stanley (1972)

Paedomorphosis in the land snail *Poecilozonites*
Hypermorphosis in *Gryphaea*
Evolutionary trends and heterochrony in
fossil invertebrates
Chesapecten (Mollusca, Bivalvia)
Ascidians
Copepods
Paedomorphosis in echinoderms
Paedomorphosis in bivalve mollusks

Plants

Guerrant (1982)

Takhtajan (1972, 1976)

Neoteny in larkspurs (*Delphinium nudicaule*)
Neoteny in the evolution of higher plants

ALLOMETRY

Mammals

Gould (1975a)

Gould (1975b)

Jerison (1973)

Pilbeam and Gould (1974)

Radinsky (1981a)

Radinsky (1983)

Roth and Thorington (1982)

Stendel (1982)

Tooth size in mammals
Allometry in primates
Evolution of the brain (review; includes all
vertebrates)
Scaling in human evolution
Skull shape in carnivores
Horse skull
Brain size in squirrels
Allometry in primates

Reptiles

Gans (1980)

Lande (1978)

Skull and brain of *Caiman crocodilus*
Limb loss in lizards

Amphibians

Hanken (1983b)

Cranial morphology in the salamander *Thorius*

Vertebrate Paleontology

Gingerich *et al.* (1982)

Marshall and Corruccini (1978)

McGowan (1973)

Prothero and Sereno (1982)

Radinsky (1981b)

Primate dentition
Dwarfing lineages
Ichthyosaurs
Dwarf rhinoceroses
Brain evolution in ungulates

FUNCTIONAL ALLOMETRY

Alberch (1981)

Alexander (1977)

Emerson (1978)

Lombard and Wake (1977)

McMahon (1973)

McMahon (1975)

Peterson *et al.* (1982)

Sebens (1981)

Locomotion in arboreal salamanders (*Bolitoglossa*)
Limbs of antelopes
Jumping in frogs
Tongue evolution in salamanders
General
Limb bones in ungulates
Tensile "skeletons"
Allometry of feeding energetics in sea anemones

D. Experimental Embryology

Experimental work requires living material and the emphasis of developmental biology has been almost exclusively mechanistic. Therefore, it is not surprising that museums have not been closely associated with the experimental study of growth and development. However, as mentioned above, recent years have experienced a rapprochement between development and evolution. In this context museum collections, as archives of diversity, can play a major role in this interdisciplinary approach. Historically, one can cite the work of Bateson (1913) on genetic, developmental, and populational variation, or the insights on gene action on development obtained by Goldschmidt (1940), with his observations on the parallel variation in wing markings between species of butterflies and phenocopies obtained in the variation. Waddington (1957, 1975) and Schmalhausen (1949) also integrated experimental work with analyses of phylogenetic patterns. This approach has been recently reviewed in the book by Raff and Kaufman (1983). Specific research results are usually based on the search for congruent patterns between experimental perturbation of a given developmental parameter and the observed phylogenetic diversity. Some examples of this approach can be found in Alberch and Gale (1983, 1985), Bard (1977), Devillers (1965), Devillers and Corsin (1968), Murray (1981), Raynaud (1981), and Tschumi (1953).

III. CURATORIAL PROCEDURES

The goal of a curator is not only to maintain collections, but also to make them as useful as possible to the scientific community. Therefore, it is imperative to use curatorial practices in collections, fixation, and preparation of embryonic material which maximize the possible usage of specimens. The following general guidelines apply to vertebrates.

A. Collection

As argued in the preceding section, and proven by the references cited, an embryonic specimen can be as useful as an adult. For this reason it is unjustified to discard eggs, larvae, or embryos. The following recommendations can be given:

If a clutch of eggs is collected, it should be accompanied by as detailed field data as possible, including description of collection site, number of eggs, size/weight, etc. In addition, it is advisable, after fixation of part of the clutch, to try to allow the remaining eggs to continue developing. If the conditions are appropriate and embryonic development proceeds normally, embryos should be preserved at regular intervals so as to obtain an ontogenetic series. One or two specimens may be allowed to hatch to assist with identification (if necessary), or as voucher specimens for the rest of the clutch. Bird eggs used to be collected, emptied, and their contents discarded. This practice has resulted in severe losses of material and the rarity of adequately preserved embryos in ornithological collections. Zusi *et al.* (1982) have reviewed and inventoried avian anatomical specimens, including embryos and juvenile material. Although no specific discussion on the issue of embryonic material is given, it addresses the importance of anatomical material in ornithology. Herpetological collections have, in general, been more sensitive regarding the value of embryonic material, and separate collections of anuran and urodele larvae often are preserved. More rarely, however, are egg clutches collected and preserved. Ichthyologists have done more work on larval biology; important and comprehensive larval collections are available which have provided the data for some major treatises on larval fishes (e.g. Fahay 1983; Jones *et al.* 1978). Historically, the largest, most important collections of larval fishes have been associated with fisheries institutions where curators had different priorities than museum curators. Most of these collections have been or are being moved into permanent museums. Recently, a symposium on ontogeny and phylogeny of fishes was held and the proceedings have been published (Moser *et al.* 1984). There is a fair amount of pertinent curation-related information in this volume.

If we are dealing with viviparous species, the collector must make sure that appropriate fixation techniques are used in the preservation of the female (see below). In the case of mammalian collections, if the adult female is to be prepared as a skin, the embryos may be preserved in fluid separately with a cross-reference.

B. Fixation

Most embryonic and larval specimens will require a fixation procedure which would allow later use as histological material, usually serially sectioned thin slides or whole mount preparations. For this reason, and the inherent fragility of embryonic tissues, embryos and larvae should be fixed with an appropriate fixative. Otherwise, the material will soften and deteriorate histologically. The most commonly used fixative, which works satisfactorily for most purposes, is formalin. Formalin appears to function as a fixative by forming cross-links between adjacent protein chains, denaturing and thus deactivating them. Autolysis is stopped and proteins are coagulated, preventing breakdown of tissues. Formalin is prepared by diluting stock formaldehyde solution (40%) to the desired concentration. The usual concentration is 10% (one part formaldehyde diluted with nine parts of water). Some ichthyological collections use 5% formalin for fixation of eggs and larvae (Fink *et al.* 1978). I have found 10% formalin adequate for fixation of amphibian and reptilian embryos at all stages. The specimens were later used for histology with satisfactory results (e.g. Haluska and Alberch 1983). *Formalin solutions must always be buffered to prevent decalcification* of the specimens. Prevention of decalcification is particularly important when dealing with embryonic or juvenile material which in general has poorly calcified elements. The acidity of unbuffered formalin will cause decalcification of hard tissues and this can be a serious problem with specimens to be cleared and stained for osteological study (see below). There are several methods to buffer formalin near a neutral pH (values between pH 6 and pH 7 are adequate). The most common and inexpensive procedure is to saturate the formalin solution with calcium carbonate in the form of marble chips or marble dust. A more controlled buffering recipe (from Humason 1979) used in my laboratory to fix small specimens to be used for histology is the following: 10% formalin - 1 liter; sodium acid phosphate ($\text{NaH}_2\text{PO}_4 \cdot \text{H}_2\text{O}$) - 4 g.; anhydrous disodium phosphate (Na_2HPO_4) - 6.5 g. The specimens may remain in this solution indefinitely. The action of the fixative is progressive.

As discussed by Taylor (1977) and Fink *et al.* (1978), borax, frequently used by ichthyologists and herpetologists, at least, is not an adequate buffering agent. Borax causes an increase in the rate of clearing in specimens.

There are other fixatives which can be used to preserve embryos which are described in any textbook of histological methods (e.g. Humason 1979). Given the hazardous nature of formalin and the inconvenience of working with specimens in this fixative, safer alternatives should be explored and tested.

When pregnant females are fixed, special attention must be given to assure adequate preservation of the embryos, since in large specimens the fixative may not penetrate fast enough to prevent decomposition. The standard procedure with lower vertebrates is to inject the abdominal cavity of the specimen with fixative. In large mammals, embalming (perfusion) is required (see description of techniques in Schultz 1924). Quay (1974) has recently presented a comprehensive review of methods to preserve bird and mammal specimens in fluid which applies to the issue discussed in this section. For large mammalian embryos, perfusion is necessary and can be performed very easily, since the umbilical cord is readily available. Simply insert a cannula in the umbilical artery and inject the preservative.

C. Storage

Embryonic or larval material is usually permanently stored in 10% buffered formalin or equivalent fixative. Formalin preserves the tissues for histology better than 70-80% ethanol (the usual storage medium for adults). If formalin is used, care should be taken to keep containers tightly closed to prevent contact with air, otherwise formalin will oxidize to formic acid, thereby weakening the solution and increasing decalcification.

D. Special Processing Techniques

Embryos, larvae, and small juveniles usually are too small to allow simple dissection. Consequently, any study beyond gross description of external morphology must involve special techniques. The most commonly used ones are serial sectioning of wax- or plastic-embedded tissues, or *in toto* staining usually accompanied by clearing. There is an enormous literature on the preparation and staining of thin sections for histology which will not be reviewed here and which can be found in any textbook on histological techniques (e.g. Humason 1979). Although some methods of preparation will require special fixation, specimens fixed and stored in 10% buffered formalin can be used for most techniques. Varying degrees of

shrinkage and distortion will occur in specimens originally fixed in 10% buffered formalin and later stored in 70-80% alcohol. However, if fixation was done properly, these specimens can still be used in serial sectioning as well as for scanning electron microscopy (see discussion and examples by Quay 1974).

E. Preparation of Skeletal Cleared and Stained Specimens

The skeletal system has been the favourite organ system in evolutionary and systematic analyses, given the temporal framework provided by the fossil record. Embryos and juveniles are mostly cartilaginous and cannot be prepared as dry skeletons. Here, I list a procedure from Hanken and Wassersug (1981) and based on techniques previously outlined in Dingerkus and Uhler (1977) and Wassersug (1976). This method has been extensively used in my laboratory on a wide variety of vertebrates with very reliable and satisfactory results. The only limitations are that the specimen must have been originally preserved in buffered formalin, and that only specimens smaller than approximately 20 cm will clear satisfactorily.

Procedure (from Hanken and Wassersug 1981):

1. Fix specimens in 10% buffered formalin for at least 2 days.
2. Skin and eviscerate the specimen. This is not necessary for small embryos. However, in general, it is advisable to scrape the skin surface to allow the alcian blue to penetrate to underlying cartilage.
3. Wash in several changes of distilled H₂O for a few hours to 2 days, depending on size of the specimen.
4. Blot excess water and place specimen in a solution of 20 mg alcian blue 8GX, 70 ml absolute ethanol, 30 ml glacial acetic acid (amount of alcian blue may be adjusted to increase staining concentration). Stain for 24-48 hours, but not longer than necessary. Cartilage will appear blue if stain is taking.
5. Blot excess stain and place specimen in absolute ethanol for 1-3 days, depending on the specimen's size. Change alcohol bath at least once.
6. Transfer specimen through a graded series of ethyl alcohol baths of decreasing concentration (e.g. 95, 75, 40, 15%), and finally into distilled H₂O for at least 2 hours. Small specimens may be placed directly from absolute ethanol into water; larger specimens may require 2-3 hours in each step.
7. Place specimen in a solution of 30 ml saturated aqueous sodium borate, 70 ml distilled H₂O, and 1 gm (~ 1/4 teaspoon) trypsin. Change solution every 2-3 days, or more frequently if it takes on a bluish color. Leave here until tissues are sufficiently macerated (*i.e.* body is limp when lifted with a forceps, or bone is visible through tissues). Do not leave here too long, as the body will eventually decompose.
8. Transfer to 0.5% KOH to which enough alizarin red S has been added to turn solution deep purple. Leave one to several days, until bones are deep red.
9. Transfer through a graded series of 0.5% KOH glycerine (e.g. 3:1, 1:1, 1:3) into 100% glycerine. Leave for at least 24 hours in each step. A few drops of 3% H₂O₂ per 100 ml solution may be added to either or both of the first two steps to de-pigment animals not initially skinned, or with remaining internal fascia. Specimens may remain bleaching for up to several days.
10. Add a few crystals of thymol or phenol to the pure glycerine to inhibit mold and bacteria.

IV. CONCLUSION

Contemporary evolutionary biology is faced with the paradox that, although there is a very well developed theory of mechanisms of change at the genetic level, the phenomenon to be explained is a morphological one. Paraphrasing Waddington (1975:vi): "Where this prescription (the Neo-Darwinian paradigm of selection acting on genes) fails to pass muster is just in problems of evolutionary adaptation at the organ or even tissue level; and these are the 'classical' problems of evolution. Moreover, they are the problems which have philosophical implications. It is doubtful if anyone would have felt any need to resist

the notion of evolution if all it implied was that the exact chemical constitution of haemoglobin gradually changed over the ages. The importance of the Theory of Evolution, as part of man's thinking about the universe in which he finds himself, is that it offered an alternative to the notion of an Intelligent Designer who has designed fish adapted to swimming fast (mackerel) or to lying flat on the bottom (plaice), birds adapted to flying in a number of different ways (hawks, sparrows, hummingbirds) or not to flying at all (ostriches), and animals adapted to live out their lives in an almost infinite variety of different ways, but always very effectively." What Waddington is talking about is the need for a theory of morphological evolution.

Morphological analysis has been mainly restricted to "equilibrium" situations (Lauder 1981), that is, a study of adaptation centered on the integration between the organism and its environment. In this approach the organism is usually viewed as an adult, static entity and the mechanisms driving morphological transformation are assumed. Therefore, classical evolutionary morphology has served mainly to provide data that are consistent with the results derived from studies at the genetic level. A challenge in contemporary evolutionary biology is to build up a comprehensive theory of morphological evolution — a theory with predictive powers and amenable to falsification, a theory that takes into account the differences in organization, nature of interactions and complexity between the genetic and morphological evolution as well as the hierarchical nature of organisms and the limits of reductionism (e.g. see Gould 1982b and Wake *et al.* 1983). Regardless of the final shape of such a theory, I am convinced that development will play a central role in it. The reasons are twofold: (1) development provides a dynamic view of the organism; and (2) it gives insights into its internal organization. An understanding of the mechanisms that generate form allows us to study the constraints imposed on the expression of phenotypic variation upon which selection can operate (Alberch 1982).

A comprehensive theory of evolutionary morphology must integrate functional and developmental components. Although both of these disciplines tend to be typological, the case is more extreme in ontogenetic studies. Developmental biology, mainly because of its non-evolutionary emphasis, as well as logistic problems relating to availability of live embryonic material, has based its studies on the mammal (rat or mice), the bird (chick), the frog (*Xenopus* or *Rana*), and the salamander (axolotl).

A developmental biology that can be integrated into an evolutionary context must include studies on the variability of ontogeny within and between groups. Museum collections can provide invaluable information in that regard. It is paradoxical, however, that museum collections have had a limited role as a source of reference for embryological work. Curators and field collectors must understand the value of embryonic and larval material. Similarly, this material and its ancillary information must be stored in a manner that allows for easy retrieval.

I would like to conclude by making the following recommendations:

1. Embryos (*in utero* or *in ovo*), larvae, and young juveniles should always be preserved and curated using appropriate procedures, which may be different from adult preservation. Large pregnant females should always be injected intraperitoneally or perfused with preservative to assure adequate preservation of embryos. When preparing a skin or skeleton of a female of a rare and viviparous species, always check if embryos are present, and remove and preserve them in the adequate fixative.

2. Liaisons between museums and zoos should be established. My experience has been that curators at zoos often are not aware of the value of dead embryonic material. Just one specimen at the right stage can have tremendous scientific importance (for example, see Rosen *et al.* 1981 and Bellairs and Gans 1983). Museum curators should contact zoo curators to arrange for the appropriate preservation of freshly dead embryonic material. In cases where a zoo has a breeding surplus of a given species, it should consider depositing in a museum a preserved and well staged ontogenetic series from egg to hatchling. It must be emphasized that field data are not essential when material is used in macroevolutionary studies and for the establishment of homologies.

3. Collectors who obtain a clutch of eggs should try to keep them alive and preserve them at regular intervals to obtain a good ontogenetic series. This raising of a clutch may be required when a juvenile is needed for positive identification.

4. Optimally, museum curators should keep a separate file of embryonic material. In practice, curators do not have the time and personnel to go through the collection systematically, pulling embryos out of pregnant females. However, eggs, larvae, and isolated embryos should either be stored physically separated from the main collection, or a separate catalogue should be maintained. Federal agencies should support these efforts, as well as the development of a centralized compilation of embryonic series

available in all the major collections. The generation of such a reference file could be performed by committees attached to professional societies. A good model may be the world-wide inventory of avian anatomical material available in museums recently prepared by Zusi *et al.* (1982). These efforts would facilitate researchers to locate embryonic material required for their studies and allow curators to respond to inquiries regarding embryonic material in their collections.

In conclusion, a concerted effort must be made to emphasize the message that organisms are not static "adult" entities but, rather, ontogenetic cycles (Bonner 1965, 1974). A modern museum should, and can, preserve this dynamic view of the organic world.

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5. MUSEUM COLLECTIONS AND MOLECULAR SYSTEMATICS

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I. INTRODUCTION

In addition to their well-known function as repositories for the storage and curation of specimens, natural history museums traditionally have been a location for biological research. Historically, scientists studying almost any aspect of the diversity of life have required extensive comparative collections. Because such material could not easily be re-obtained whenever desired, its storage for the use of future workers was necessary (Staflou 1969). This led to the use of museums as a place of storage, not only for type specimens, but for other voucher specimens, for historically important dissection materials, for documenting the extent of variation, *etc.* Even before scientists began to accept the idea of evolution in the last century, museum collections were used for the investigation of hierarchies of taxa, biogeography, ontogeny, anatomy and morphology. In fact, because of the need for large quantities of comparative material for studies of patterns and theories of the variability, diversity, and relationships of biological organisms, natural history museums have been the primary locale for scientific studies of systematics (*e.g.* Mayr 1942; this volume). Such studies have incorporated a great diversity of methodologies and techniques.

In the last 10 to 15 years, molecular techniques have increasingly been used as tools by museum researchers in systematics. The particular methods have varied with the taxonomic group and the taxonomic level of the problem being addressed. But, however intricate, all these biochemical and other molecular techniques are aimed at revealing new systems of characters to be analyzed. There is nothing inherently superior about the results of this research, compared with more traditional morphological or other phenetic studies. The data obtained (a set of character states or a measure of the phenetic resemblance of taxa) must be analyzed and interpreted in terms of relationship or other evolutionary patterns. Molecular characters must be evaluated on the basis of the quality of the results, and of the insights into evolutionary pattern and process they provide. The actual advantages of these newer methods are associated with the fact that they represent an entirely new set of characters, and so may offer a fresh view of traditional problems. Additionally, at least some of the newer methods enable one to examine rapidly many characters for many individuals or species using automated or semi-automated technology.

It is not obvious that the addition of molecular approaches to the techniques already in use by museum workers represents any fundamental break with tradition. Over the last 50 years systematists have added increasingly powerful microscopes, measuring instruments, tape recorders, statistical tools including computers, and other devices to their research arsenals. Means to generate biochemical characters are nothing more than a continuation of this trend. However, a difference which is important to some systematists is that certain biochemical techniques take one to the level of genic events (Frelin and Vuilleumier 1979). This is a distinct advantage to systematists who are interested in population genetics and microevolution; however, to those not particularly interested in these areas biochemical character sets can be treated as any other set. Frequently, biochemical methods have been developed and first used in university laboratories by persons not trained in traditional systematics. However, this is no reason why museum workers can not profitably use the methods also. It is not necessary to be a trained biochemist to use these techniques; in addition, most biochemists do not have the necessary background to know which taxonomic problems are really interesting, or how useful a method actually will be in practice. In this regard, collaboration could be profitable. Many, if not most, of the significant, detailed contributions to systematic knowledge deriving from application of these new techniques have come from museum and collection-oriented specialists.

II. COLLECTION AND CURATION OF BIOCHEMICAL MATERIAL

Traditional methods of collecting and preparing organisms differ according to both taxonomic groups and the purpose for which the specimen is intended. For example, different procedures are used for field preparation of study skins, skeletons, and spirit specimens of vertebrates such as birds and mammals. This is also the case with field-preparation techniques for organisms intended for use in molecular studies. Specimens to be used for eventual protein analysis usually must be frozen. DNA studies may require preservation in alcohol or freezing, depending upon how the nucleic acids will be utilized. Karyological work requires either bringing cells back alive (as captive specimens or *in vitro*), or some relatively intricate field laboratory work.

Needless to say, advice on both field and laboratory techniques or, better still, apprenticeship, is essential before undertaking a research project using molecular techniques.

A. Proteins

Most systematists working with proteins analyze these molecules electrophoretically or immunologically. A small amount of amino acid sequencing and peptide mapping has also been done. The most efficient field methodology for saving tissue for any of these techniques is freezing. Samples are best kept as cold as possible; liquid nitrogen is routinely used by many workers. Dry ice is acceptable, but must be replenished much more frequently; modern liquid nitrogen dewars will remain cold for several months on a single filling. Very small organisms, such as *Drosophila*, may be frozen entire in a labelled vial (but desiccation may become a problem with long-term storage of small samples). Liver, kidney, heart, blood, etc. are saved from larger specimens. In the museum the material must be kept continuously cold until used. Ultra-cold freezers (-70°C) are ideal for this purpose.

Naturally, it is extremely important that tissue samples, for protein or DNA work, be unambiguously labelled and stored. Museum workers are aware of the need and procedures for careful labelling, cataloguing, and curating specimens. It is also important to have traditional voucher specimens, labelled accordingly, to document the tissue samples.

The literature describing electrophoretic techniques is extensive. Brewer (1970), Shaw and Prasad (1970), and Selander *et al.* (1971) can be consulted for recipes. Avise (1974) discusses general aspects of the use of electrophoresis in systematics. As with other biochemical techniques, some examples are cited in the next section of this chapter. The immunological approach to micro-complement fixation is described in Champion *et al.* (1974).

B. DNA

DNA, for dissociation/reassociation (DNA hybridization) studies may be collected and preserved indefinitely in 80-85% ethanol (Sibley and Ahlquist 1981a). Frozen tissue samples, especially liver, have been used for mitochondrial DNA restriction mapping (mtDNA). However, Lansman *et al.* (1981) found

that fresh material gave substantially better yields. This requires bringing specimens back to the laboratory alive for immediate analysis or for starting tissue culture lines (see below).

The technique of DNA hybridization has been described in some detail by Sibley and Ahlquist (1981b). Lansman *et al.* (1981) describe a mtDNA technique.

C. Chromosomes

Animals caught alive in the field can be karyotyped immediately through the colchicine injection technique (see Patton 1967). An alternative method which produces better results is to culture tissues from live animals brought back to the laboratory, where tissue cultures can be started (Shields 1983). The chromosome spreads are stored on microscopic slides; additionally, photomicrographs may be prepared and filed.

White (1978a) offers a general review of chromosomes, and the differential staining techniques have been described by Shields (1983) among others.

D. Collecting

As with traditional museum collecting, no single person can collect adequate material for major studies rapidly or efficiently by him- or herself (Foster 1982). Cooperation among museums and researchers is necessary and some general collecting to gather molecular samples for future use is warranted. Eventually it is likely that trading tissue and other samples for biochemical work will be as routine as is the current trading and loaning of standard museum specifications. If time is available and permits allow, researchers ought to save tissues whenever possible. All the arguments that apply to the need for traditional collecting — inadequate sample sizes, incomplete data and poorly labelled specimens, the rapid destruction of little known biotas, etc. — apply to molecular collecting as well. Only museum scientists are trained professionally to perform such work, and it is mainly their responsibility to document the molecular diversity of life while it still exists. Because of the general decline in training in museum collection-techniques, and the difficulties of adequate sampling of widespread taxa, there is currently an increasing interest in collaboration among museum researchers doing molecular work. This is true of ornithology, for example, where a number of joint projects are currently underway.

III. SOME ILLUSTRATIVE RESULTS

Molecular studies have been used at many different levels of the taxonomic hierarchy, ranging from studies of the extent of genic variation within populations to comparisons of homologous proteins among kingdoms. Techniques exist that will expose useful variation at any of these levels, but which of these is most appropriate depends upon the specific problem and the taxa of interest.

A. Intraspecific Studies

Ever since Darwin's work, evolutionary biologists have been aware that the amount of variation present within populations is important for understanding details of evolutionary processes. Description of the extent of morphological variation present within populations has been frequent; for example, most studies of geographic variation of species also have included such analyses (see Chapter 6). But, as discussed by Lewontin (1974), the evolutionary importance of such phenotypic variation is unknown due to several potential biases. First, the characters that vary may not be a random sample of all characters and, second, unless breeding studies are carried out and heritability is calculated, the actual relevance of phenotypic variation for evolution remains unknown — the variation might be environmentally induced (James 1983). Molecular methods may get around these particular problems, however.

In most cases there is a relatively simple relationship between a biochemical pattern and an organism's genotype. This is because the molecules most frequently used in biochemical systematic studies are either chromosomes themselves, or the translated products of chromosomes — proteins. Furthermore, the examination of this variation is not biased a priori — one can search for the variation without advance knowledge of its existence. Thus electrophoretic surveys of variation (measured as heterozygosity — Nei 1978) have become popular. A review can be found in Nevo (1978).

Substantial differences in the extent of intraspecific variation exist among taxa. Some investigators have posited that this variation is related to variables such as ecology, social behaviour, physiology, etc., and have investigated the topic through correlation. Other workers, the so-called "neutral" school, have assumed that this variation is not of evolutionary importance *per se*, but that it reflects such parameters as population size, time, and mutation rates. Some specific predictions of the latter position have been upheld (Chakraborty *et al.* 1980). In any case, quantification of molecular variation has revealed a previously unknown aspect of populations. Some of the results have surprised investigators. For example, a very old form of life, the horseshoe crab *Limulus*, is about as variable as more recently derived taxa (Selander *et al.* 1970). Other results have been of ecological and evolutionary interest, for example, Bonnell and Selander (1974) found that Northern Elephant Seals (*Mirounga angustirostris*), which went through a bottleneck of population numbers around the turn of the century, were invariant at all genetic loci examined. These and other results are summarized in Selander (1976). For museum workers interested in questions associated with the description and investigation of the variability of populations, the examination of genic heterozygosity has become almost essential. While the early work in characterizing the extent of genic variation in natural populations was done by population geneticists, recent surveys, such as that of Nevo (1978), have relied to a major extent on the work of specialists who incidentally reported on genic variation as a part of their systematic investigations.

B. Interpopulational Variation

Studies of geographic variation, including descriptions of subspecies, clines, and the differentiation of allopatric populations, traditionally have relied on morphology for a source of characters (see Chapter 6). The interpretation of patterns of this variation has always been ambiguous to some degree because of the potentially confounding effect of environmentally induced variation. For example, clinal variation in body size, appendage length, and colour have been interpreted in terms of such ecomorphological generalizations as Bergmann's rule, Allen's rule, etc., with the supposition of a selective (*i.e.* adaptive) basis. However, other classic studies, especially in plants (Clausen *et al.* 1940; see also James 1983), showed that some geographic variation was environmentally induced, or at least the result of gene-environment interaction. Thus, molecular studies of geographic variation have become of considerable interest to systematists because of the potential they offer to clarify the separate contributions of genotype and environment.

Because of their known genetic basis, patterns of allelic frequency differences over the range of a species can be interpreted in terms of gene flow, natural selection, and random drift due to limited population size. In many cases, patterns of allelic frequency variation over species' ranges seem to reflect mainly distance and isolation. Clines in allelic frequencies have been found in numerous taxa, including crustaceans (Corbin 1977), fish (Merritt 1972), birds (Sibley and Corbin 1970), and mammals (Selander *et al.* 1971). The geographic scale has varied greatly in different studies. Ayala *et al.* (1974) have surveyed the frequency of electrophoretically detected alleles in the *Drosophila willistoni* group across much of the Americas. Highton and Webster (1976) found widespread uniformity of allelic frequencies in the salamander *Plethodon cinereus* north of the southern limit of glaciation in eastern North America, but extensive variation of frequencies south of that line. Patton and his colleagues (Patton and Yang 1977; Patton and Feder 1981) have investigated micro- and macrogeographic variation in pocket gophers of western North America (*Thomomys*) using electrophoresis and karyology in addition to traditional skin and skull characters. The patterns of allelic and chromosomal variation in these rodents were interpreted in terms of geographic distance and vagility of the animals. Several hybrid zones in this taxon also have been discovered using molecular methods (*e.g.* Hafner *et al.* 1983). The authors have used the molecular data sets to clarify the taxonomic situation in this notoriously complicated, polytypic taxon and, at the same time, have made a major contribution to ecological and evolutionary genetics.

One of the advantages of molecular techniques is the possibility of rapidly examining a number of different genetic loci. The results of multiple locus electrophoretic surveys can be summarized by measures of the genetic distinctness of geographically separated populations. For example, Wright's F_{ST} statistic (Wright 1978) gives an estimate of the degree of isolation of local demes with respect to the entire population of a species. The statistic can be calculated for multiple hierarchical levels and hence be used to investigate topics such as whether subspecific designations are justified on genetic grounds, and whether apparent geographic barriers are really effective in isolating populations. Concordance of morphological and biochemical characters indicates that well marked forms represent different gene pools or genetic

stocks. Thus, analyzed in this fashion, biochemical results give direct information on the genic continuity of a species, something phenetic and morphological surveys aspire to but can only address indirectly. Such results, a measure of the genetic structure of populations, have been summarized for several groups of vertebrates by Barrowclough (1983). Electrophoretic investigations of geographic variation can provide museum specialists with a new perspective on the population structure of their groups. The calculation of F_{ST} statistics also has become interesting because the genetic structure of populations is one of the important variables influencing modes of speciation (Templeton 1980). Here again, museum workers are making major contributions to another field, population genetics, as a by-product of their own work.

C. Speciation

Different concepts of what constitutes a species are prevalent among taxonomists working on different major groups of organisms. However, in most cases the criteria are related to ideas such as reproductive isolation, evolutionary lineages, and morphological distinctness. These concepts are closely related because in order to be morphologically diagnosable, populations almost certainly have to be reproductively isolated (e.g. cannot be clinally connected), and reproductively isolated populations of necessity will have their own evolutionary history. However, troublesome intermediate cases always exist and will be interpreted in somewhat different ways by proponents of different schools of thought. Molecular methods will be of value to researchers who are interested in the processes of speciation and in the specific status of populations.

1. Species Status

The determination of species status using molecular techniques principally involves a search for constant (i.e. fixed) genetically based differences between the taxa of interest. The genetic differences may involve proteins or chromosomes. The underlying theme, as mentioned above, is the idea that fixed genetic differences between two samples imply a lack of reproductive continuity between the organisms and, hence, the presence of two species. Fixed differences in proteins among organisms mainly have been sought using electrophoresis. Constant chromosomal differences can be found using karyotyping, and, in many cases, banding has not been necessary if the objective was simply to ascertain the presence or absence of gross differences.

One of the first results of this sort of analysis was Manwell and Baker's (1970) discovery of a previously unsuspected cryptic species of sea cucumber (Holothuroidea) using electrophoresis. Two distinct mobility patterns were found with no intermediates (heterozygotes), thus strongly indicating the existence of two different species. Similar kinds of electrophoretic results have supported the existence of hitherto unrecognized species in a number of other taxa, including amphibians (Highton and Webster 1976), birds (N.K. Johnson, pers. comm.), and mammals (Patton *et al.* 1976). In an analogous fashion, karyotypic differences have demonstrated the existence of previously unknown or ambiguous species in a number of taxonomic groups, including insects (White 1978a), amphibians (Uzzell 1964), and mammals (Patton and Feder 1978). Thus, the search for molecular differences between putative species pairs, or searches for unknown sibling species in morphologically difficult groups, is a potential tool of major significance for museum researchers. Unfortunately, however, the technique cannot be regarded as definitive because the apparent absence of a fixed difference does not demonstrate that a sample consists of only one species. Speciation does not ensure immediate biochemical differentiation. Thus negative results are uninformative.

2. Processes of Speciation

The use of electrophoresis to study mechanisms of speciation, albeit widely touted, has not been markedly successful. There is an empirically observed increase of genetic distance with taxonomic level, e.g. genetic distances among local populations average less than those among subspecies which, in turn, are less than those among species, etc. However, the principal import of this observation is that genetic distance increases with both geographic distance and with time. This leads to the inference that speciation may be related to geographic separation and time of isolation. Such generalizations were made years ago on the basis of morphological studies (e.g. Mayr 1942). There have been a few studies of allelic frequency variation across hybrid zones (e.g. Dessauer *et al.* 1962; Hunt and Selander 1973; Barrowclough 1980; Hafner *et al.* 1983). Some of these authors have interpreted the patterns in terms of cline theory to get indirect estimates of the magnitude of selection operating in the hybrid zone. While such studies are of

great interest because of the information they impart concerning the dynamics of gene flow and selection in natural populations, they do not convey information concerning the nature of the processes responsible for the initial development of the differences, genetical or morphological, between the two taxa.

Perhaps the most interesting of the studies involving speciation using molecular methods are those on salamanders using electrophoresis, and on mammals using karyotypes. Wake and colleagues (Wake 1981), in a series of studies of speciation and geographic variation in *Batrachoseps* and *Ensatina*, have found several cases of a lack of concordance between patterns of coloration and electrophoretic genotypes. Major allelic frequency differences or fixations among populations of salamanders with the same phenotype suggest that phenetic differences are not directly associated with speciation. The addition of this independent biochemical character set has added much new information on the specific status and age of salamander populations in these studies, and has made it clear how much more complicated is the biological situation in these western North American amphibians than was previously thought. The taxonomy of these salamanders will be substantially altered as a result of the investigation of their evolutionary genetics by a museum morphologist.

Mammalogists now routinely karyotype their organisms in the course of studies at the species level. In mammals, there is frequently a correlation between species status and karyological differences. This has led some authors (White 1978a, b) to postulate that, in a number of major taxonomic groups, the predominant mode of speciation may be stasipatric chromosomal evolution. That is, speciation may be the result of the origin and spread of new karyotypic forms in small, inbred populations. Such new chromosomal arrangements are postulated to be as fit as the old arrangement when homozygous, but at a selective disadvantage while heterozygous. Such a process has been suggested for rodents of the genus *Mus* (White 1978b), and bats of the genus *Uroderma* (Baker 1981; Greenbaum 1981). However, the interpretation of data used in support of this mechanism remains arguable (Hafner 1982); it is now apparent that is going to take relatively sophisticated mathematics and statistical analysis of large samples of data to distinguish decisively between this mechanism and an alternative explanation of hybridization due to secondary contact. At any rate, karyological and biochemical methods have made feasible the investigation of alternative processes of speciation not previously yielding to qualitative investigations. Museum workers have been most vigorous in pursuing this field of research.

In spite of these advances, however, significant progress in the explication of the details of speciation has not been rapid. Rather, the more usual result has been that investigators have come to realize that the interpretation of a particular biological situation is considerably more complicated than previously thought. The predominant mechanism of speciation may well vary with taxonomic group and be a function of vagility, deme size, and social behaviour (Lande 1980; Templeton 1981).

D. Phylogenetic Relationship

Major effort has been devoted to molecular studies of phylogeny in a wide array of taxa using a variety of techniques. This work dates back over half a century and, to a large extent, has been associated with museums and museum researchers.

Comparative chromosomal studies of *Drosophila* were being performed in the 1920s (Patterson and Stone 1952). Chromosomal phylogenies, based on this work, appeared as early as 1937. Because the logic and mathematics of phylogenetic inference have only recently been the subject of intensive investigation (e.g. Sneath and Sokal 1973; Hennig 1966; Farris *et al.* 1970; Felsenstein 1981), such early studies may not live up to present standards, but nevertheless were pioneering in their own right. Phylogenies based on karyotypes using improved techniques and methods of analysis have been reported for a number of vertebrate taxa, including lizards (Cole 1970), birds (Stock and Bunch 1982), and rodents (Yates *et al.* 1979).

Studies of proteins, using a wide variety of biochemical techniques, have been the most popular approach to molecular phylogenetic research. Sequencing of amino acids in proteins has been quite useful. Appropriate choice of a protein allows one to examine problems at almost any taxonomic level. For example, histones, conservative proteins associated with DNA, evolve very slowly, and homologous amino acid residues have been found throughout the kingdoms of organisms. In other proteins substitutions are quite frequent and these molecules can be used for intergeneric studies. The best known sequencing studies are probably those of cytochrome c. Using these sequence data, Fitch and Margoliash (1967) were able to derive a phylogeny for a variety of vertebrates that was in general agreement with what was known on the basis of anatomy and morphology.

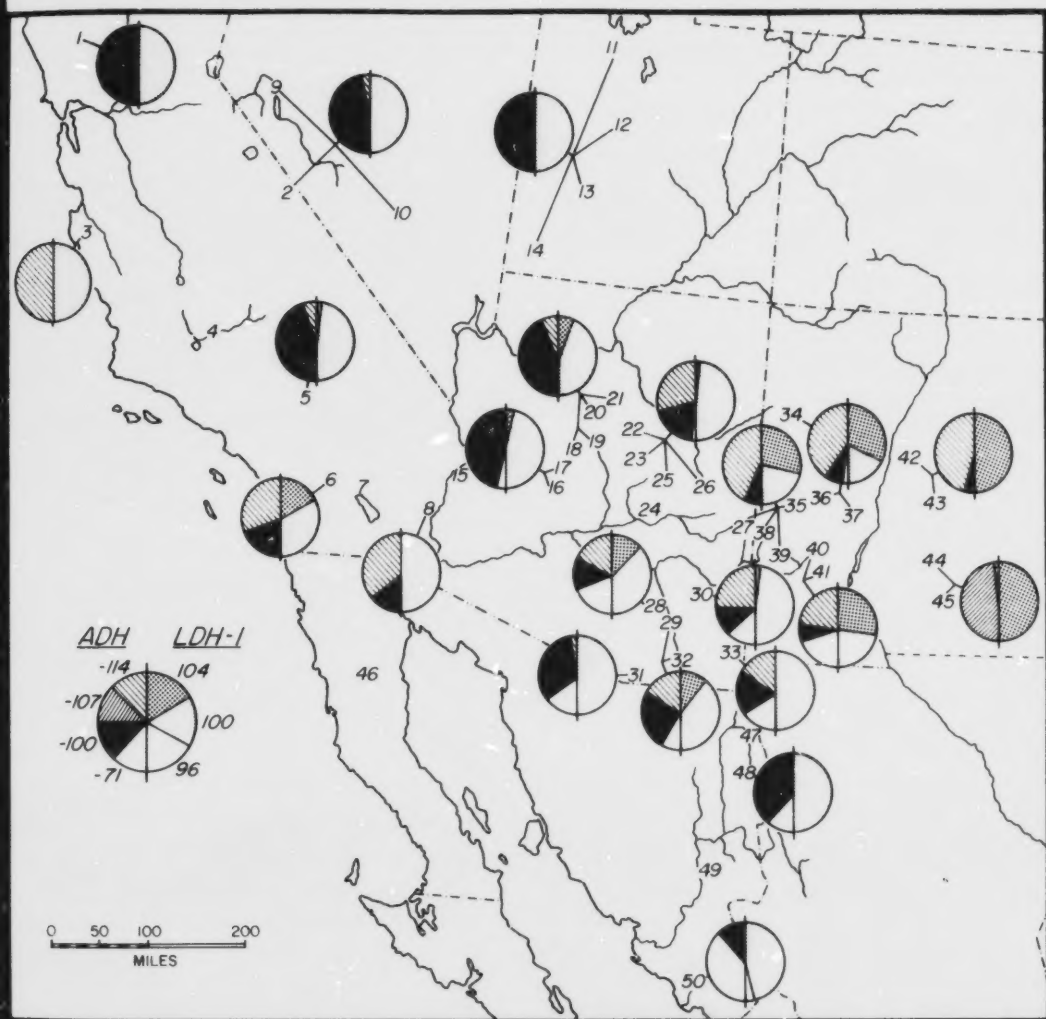


Fig. 1. Allelic frequency variation across the southwestern United States and northwestern Mexico at two genic loci in the pocket gopher, *Thomomys bottae*. The alcohol dehydrogenase (ADH) and lactate dehydrogenase-1 (LDH-1) loci were examined in population samples using electrophoresis. On the basis of these and other genic loci, two major geographic divisions of the populations were identified: northwestern (California and Nevada) and southeastern (Arizona, New Mexico, and Mexico) subdivisions. (From Patton and Yang, 1977, Fig. 3.)

Sequencing the amino acids in specific proteins has been done principally in biochemistry departments and not in museums. However, most other methods of characterizing proteins, including studies of immunology, molecular weight, electric charge, isoelectric point, and peptide mapping have all been performed by museum researchers. Probably the greatest successes of these methods have occurred when investigators have applied them to taxa of uncertain affinities, or to problems of the relationship of higher-level taxa (genera, families, and above) that remain ambiguous using more traditional systematic tools. It is the museum specialist, with detailed knowledge of the taxa, not a biochemist or geneticist, who undertake such studies. For example, using the immunological technique of microcomplement fixation,

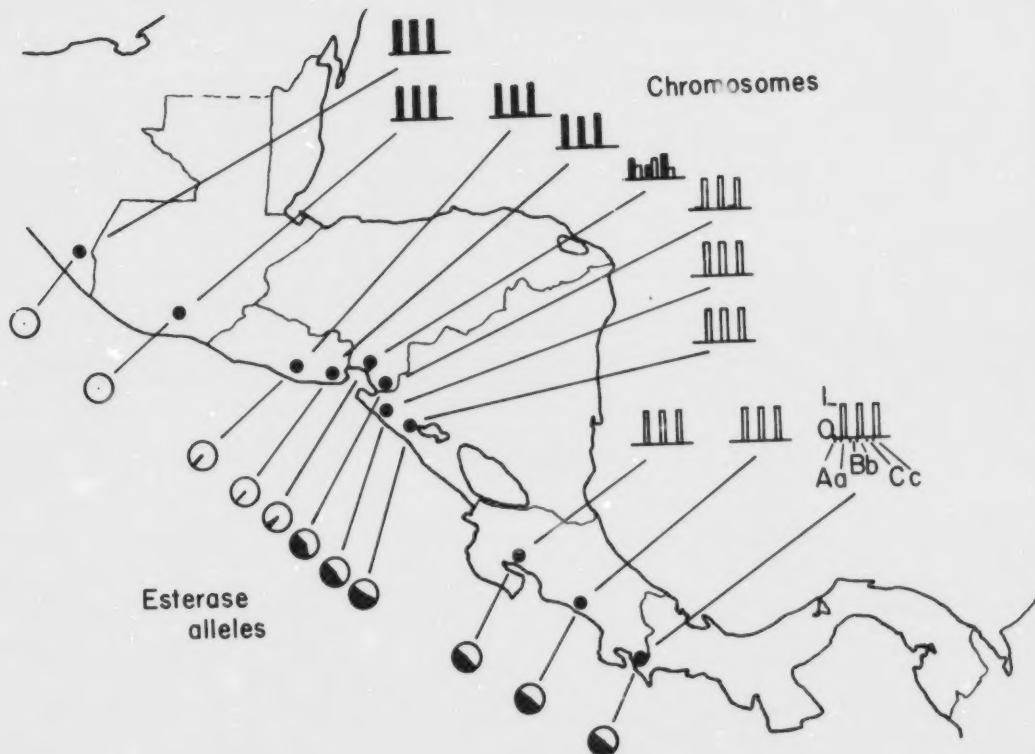


Fig. 2. Variation of chromosomes and genic loci in a narrow hybrid zone in the tent-making bat (*Uroderma bilobatum*). Three chromosomal polymorphisms and two alleles at the esterase-2 locus vary in concordance in a transect through Central America. The two taxa are indistinguishable except by molecular techniques; nevertheless, the karyotypic differences suggest these represent two distinct evolutionary lineages. (After Greenbaum, 1981.)

Cadle and Sarich (1981) analysed snake albumins and discovered that the New World coral snakes (micrurines) are related to Old World elapids rather than to New World colubrids.

Electrophoresis has been the single most commonly used technique for studying relationships using proteins. Yang *et al.* (1974) worked out the phylogenetic relationships of the *Anolis* species on the Lesser Antilles using starch-gel electrophoresis. They then used the results to discuss the evolutionary history of colonization and speciation in this archipelago. Gutiérrez *et al.* (1983) used starch-gel electrophoresis of proteins to determine the phylogenetic relationships within and among some genera and families of galliform birds. Straney (1981) estimated relationships among families of New World bats using the same technique. Among the surprises coming out of this work was Sibley's (1968) discovery that the enigmatic wren-thrush of Costa Rica and Panama is neither a wren nor a thrush, but a member of the New World nine-primaried oscine assemblage. At a lower taxonomic level, H.C. Dessauer and C.J. Cole (pers. comm.) were able to work out the precise crosses giving rise to specific clones of uniparental *Cnemidophorus* lizards, again using starch-gel electrophoresis.

Little work has been published on peptide-mapping as an indicator of relationship. Corbin (1968) investigated relationships in the avian order Columbiformes using tryptic digests of ovalbumin.

Recently, studies of DNA have become of particular interest. Sibley and Ahlquist (1981b, 1982) have improved the DNA-DNA renaturation techniques (DNA hybridization) of Shields and Strauss (1975), and performed extensive studies of phylogeny of birds at the level of families and orders. They have had

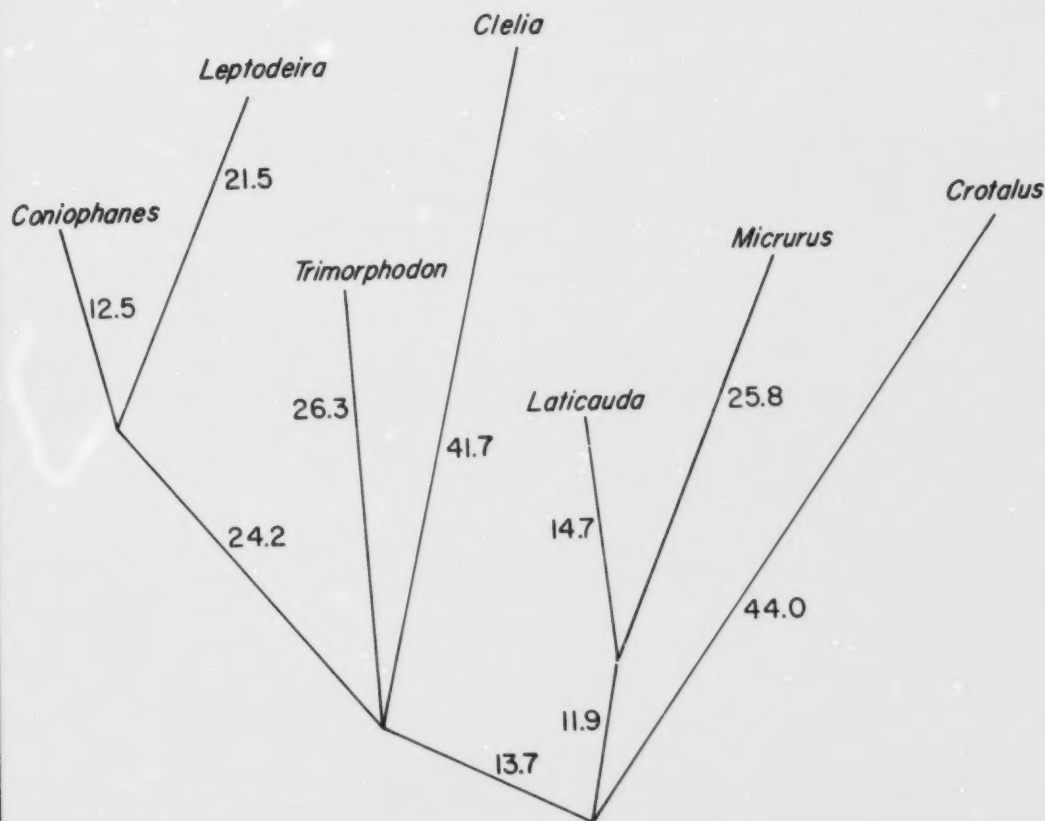


Fig. 3. Phylogeny of several genera of snakes based on the immunological technique of microcomplement fixation of serum albumin. The relationships of the New World coral snakes (*Micrurus*) are with the Old World elapids (*Laticauda*) rather than with the New World colubrids (*Trimorphodon*, *Clelia*, *Leptodeira*, and *Coniophanes*). Branch lengths are given as immunological distances. (After Cadle and Sarich, 1981.)

good success at elucidating the relationships of passerine families that were previously just listed in standard classifications without implied phylogenetic relationship. Of great interest is their discovery of large assemblages of families within this order that make substantial zoogeographic sense (Sibley and Ahlquist 1984).

Mitochondrial DNA restriction fragments have been used to infer a phylogenetic tree for primates (Ferris *et al.* 1981; Templeton 1983). Lansman *et al.* (1981) have used the same technique to investigate matrilineal genealogies for a pocket gopher (*Geomys pinetis*). This technique is just starting to be taken up for detailed systematic studies.

IV. NEW DIRECTIONS

During the last two decades most researchers have used either the newer biochemical techniques or traditional systematic methods. Few used both, but this has been changing. Systematists have begun to realize that comparisons of the results of the two types of studies are interesting: concordant patterns based on biochemical and morphological methods suggest a uniformity of evolutionary change; discordant patterns indicate an uncoupling of genic and morphological variation and inconsistency of evolutionary rates. Consistent patterns of geographic variation using different suites of characters suggest the

existence of multiple evolutionary lineages. Furthermore, from a purely taxonomic point of view, such comparisons may be informative to systematists about the nature and relative utility of different characters.

Studies involving multiple sets of characters have only recently started to appear in the systematic and evolutionary literature. Mickevich and Johnson (1976) inferred phylogenies for fish of the genus *Menidia* using both morphological and electrophoretic data sets. General concordance of the resulting trees was found. Larson (1980) and Larson *et al.* (1981) examined mechanisms and rates of morphological change in salamanders by comparing the degree of morphological differentiation in a clade of these amphibians to a phylogenetic tree based on electrophoretic data. Barrowclough (1983) examined rates of morphological, plumage, and structural genic evolution in Galapagos finches by comparing morphometric, spectrophotometric, and electrophoretic data sets. Patton's series of pocket gopher studies have used karyological, electrophoretic, pelage, and morphometric data in examining the patterns and causes of variation in these animals.

V. SUMMARY

Molecular methods represent a wide variety of techniques, of varying complexities, for revealing new systems of variation in systematic studies. While not inherently superior, they may nevertheless offer the fresh perspective on old problems that comes with an entirely new set of characters. Some of these newer techniques have allowed the quantitative investigation of previously unassailable problems of evolutionary mechanisms. Museum researchers can profitably add many of these techniques to their set of systematic tools; which particular methods will be useful will depend on the nature of the problems being investigated. These techniques have already resulted in substantial advances in some museum-based systematic and taxonomic studies. In addition, museum workers have made significant contributions to the fields of population, evolutionary, and ecological genetics in the course of their systematic activities.

Molecular techniques are becoming increasingly important in museum research. They are likely to be more so in the future. In order to have adequate samples available when they become necessary, it is important that curators begin now to collect, preserve, and curate material for molecular research. Because molecular studies frequently complement traditional ones, molecular material should be saved from the same series and, if possible, from the same individuals as those prepared as traditional specimens during collecting. As taxonomic studies and revisions come to be based more on biochemical results, specimens without such associated material will be of reduced value. Saving samples for molecular studies is usually not a difficult logistical problem.

The latest directions in molecular systematic research, studies of the concordance of phylogenies based on biochemical and traditional data and studies of the uncoupling of morphological and molecular evolution on both micro- and macro-evolutionary scales, have been mainly associated with research museums. Museum-trained specialists are familiar with current evolutionary problems and with standard morphological techniques, and both are essential for this area of research. Intensive research programs combining systematics with evolutionary and ecological genetics have been at the forefront of this new field. Examples in which museum workers have made outstanding contributions in multiple areas of research include the studies of salamanders by Wake and colleagues and of pocket gophers by Patton and his students.

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6. MUSEUM COLLECTIONS AND THE STUDY OF GEOGRAPHIC VARIATION

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I. INTRODUCTION

Geographic variation has been defined succinctly by Mayr (1963: 297) as "the occurrence of differences among spatially segregated populations of a species." It is a characteristic phenomenon of the majority of continental species (Endler 1977), but is also evident at the level of adjacent local populations or demes, where it is generally referred to as microgeographic variation.

The phenomenon of geographic variation was originally discovered from the comparison of homologous characters in widely separated populations. Although records of geographic variation precede the Linnaean period (Mayr 1970), the phenomenon itself did not provoke exceptional interest among systematists until the last century when collections had grown large enough to encompass specimens from substantial portions of species' ranges. Thus from its inception the study of geographic variation has been a collection-based museum discipline.

The existence of differences among populations, especially among organisms inhabiting the Galapagos Islands, figured prominently in Charles Darwin's thinking about the evolution of life and

ultimately became an integral part of his theory of the origin of species by natural selection. The challenge to the Darwinian thesis mounted by the mutationists in the early 1900s was quelled in large part by concurrent studies of geographic variation. The gradational nature of interpopulational variation, the increase of phenetic differences with increasing distances among populations, and the demonstration of a genetic basis for even small differences among so-called geographic races of a species, were direct contradictions of the mutationists' hypothesis of the origin of species by macromutations (see Mayr 1963 for further details).

In this century a primary focus of many systematists has been to document geographic variation and to assess its evolutionary significance (Mayr 1942, 1963). The description of differences among populations of a species, and their geographic patterning, are now included routinely in systematic studies of species taxa.

Studies of geographic variation continue to be of central importance to biologists, because the differentiation of spatially segregated populations of a species is thought to be a primary event in the evolutionary process. The study of such differentiation has therefore played a prominent role in the continuing controversy on modes of speciation (allopatric, sympatric, parapatric), and has led some researchers to question the very nature of species (Sokal and Crovello 1970; Sokal 1973). In a critical review of the description and causal analysis of geographic variation, Gould and Johnston (1972: 489) concluded that the biological species concept would be in serious jeopardy if phenetic and genetic studies of geographic and temporal variation demonstrate that "gene flow cannot maintain the cohesion of local populations into a larger interacting unit."

A major premise of the modern synthetic theory of evolution is that cumulative microevolutionary changes (principally allelic substitutions) are sufficient to explain speciation and macroevolutionary trends at higher levels of organization (Huxley 1942; Dobzhansky 1951; Bock 1970; Sokal 1978). Parenthetically, the large amounts of genetic variation within and among populations discovered recently by molecular systematists (see Chapter 5), and its implication of selective neutrality of allelic substitutions, have led to an attack on the modern synthesis as an exclusive proposition (Gould 1980a, b, 1981, 1982). In this view macroevolution does not result from gradual adaptive transformations of populations, and speciation does not always arise from the slow accumulation of allelic substitutions in isolated populations at the periphery of a species range (but see Orzack 1981 and Mayr 1982 for a defence of the modern synthesis). Not only have genetic and phenetic studies of geographic variation provided the impetus for these debates, but future refinements will ultimately clarify our understanding of evolutionary mechanisms.

The literature of geographic variation is enormous, and in this review I will make no attempt to survey it all. Instead I will concentrate on studies with which I am most familiar, and which adumbrate the major features of interpopulational variation and covariation. The central role played by museum collections is implicit in most of the research reviewed below; I have not detailed this role in most cases.

II. ANALYSIS OF GEOGRAPHIC VARIATION

A. Analytical Goals and Requirements

1. Subspecies

The analysis of variation among populations is fundamental to modern systematic methodology (Baker 1975). Until about 1950, however, most studies of geographic variation had the delineation and formal recognition of subspecies as one of their goals. Although Wilson and Brown (1953) convincingly debunked this practice, Michener (1969: 232) noted 16 years later that there was still a tendency among workers to let recognition of subspecies replace genuine studies of variation in relation to geography, ecology, or chronology. He urged young systematists "to investigate such variation intensively because of its importance to evolutionary biology, but to do so not by subjective recognition and delimitation of types . . . Instead, the studies should be of the variation of individual characters . . . over the whole range of a species." In a comprehensive review of systematics and speciation in birds, Selander (1971: 75) denounced the practice of intraspecific fractionation in geographically variable species as "impressionistic, typological, and 'intuitive' systematics."

The recognition of subspecies inevitably produces the analytical dilemma of how to objectively define these taxonomic units within a clineally varying species, especially when contiguous samples are not

available over its whole geographic range. It is difficult to decide whether to attribute observed phenetic or genetic gaps to phenomena such as restricted gene flow and ecogeographic adaptation, or to inadequate sampling (Baker *et al.* 1978).

Nevertheless, the practice of describing new subspecies continues as a museum-based activity today (e.g. Clancey 1974), principally on the justification that it is a convenient pigeon-holing device for practising curators, while also serving as a preliminary analytical tool for more sophisticated analyses of geographic variation (Zusi 1982). While there may be some merit in giving subspecific rank to well differentiated populations on islands, for example, it is clear that the practice should be abandoned for continuously distributed populations with clinal patterns of variation because the resultant taxonomy actually impedes systematic analysis (Moreau 1957; Selander 1971).

2. Sampling of Specimens

One of the critical requirements of any study of geographic variation is the adequate sampling of specimens from a set of localities representative of a species' range. A good sampling design requires the collection of enough specimens from each sample locality (each locality representing a local population) to allow reliable estimation of local variation, and the sampling of enough localities to allow characterization of major trends in among-population differentiation (Pimental 1958; Gabriel and Sokal 1969; Thorpe 1976). The question of what constitutes an adequate sample size has to be answered in terms of the statistical parameters being estimated, usually means and variances (with associated covariances and correlations). For morphometric and probably most other phenetic characters, samples of 30 or more specimens at each locality are usually adequate to give stable estimates of means, although stable solutions to multivariate analyses of variance-covariance matrices probably require much larger sample sizes (around 100 specimens/locality), especially for the characterization of subtler trends uncorrelated with a general factor (Power 1971; Gibson *et al.* 1984). For characters with high within-population variances, such as the patterning of syllables of some songbirds (Baptista and King 1980; Wiens 1982), substantially greater samples may be required than with more traditional morphometric characters.

Sampling effort will also differ with the level of resolution required. For macrogeographic studies, the major emphasis in sampling will be to collect over a broad range at approximately equal intervals. For microgeographic studies, sampling error due to local variation can be a serious problem, so sample sizes must be increased (50 or more specimens are usually required), and the set of localities must be sampled on a much smaller interval or latticework (see Sokal *et al.* 1971; Highton 1977).

In many species the geographic distribution of populations in terrain now inaccessible, the temporary decline or disappearance of populations of cyclic species from parts of the range, or the lack of funding for systematic studies precludes some or all of the above sampling requirements. In such circumstances it is common practice to pool data from several contiguous localities to produce a compound locality with an adequate sample size (e.g. Hagmeier 1958; Power 1970; Reymont 1961; Yang and Selander 1968; Baker *et al.* 1978). Pooling must be done carefully and without *a priori* bias on biogeographic or taxonomic grounds (Pimental 1958; Sokal 1965; Hiernaux 1972). In general, pooling should be restricted to geographically contiguous localities in close proximity, to prevent within-sample variation from obscuring major trends in geographic variation among samples.

3. Selection of Characters

In assessing the differences among populations of a species, two problems arise in the selection of characters for study: (1) how many characters should be studied to adequately represent differences among samples; and (2) what characters should be studied? Standard justifications for using large numbers of characters have their genesis in the philosophy and practice of numerical taxonomy (Sokal and Sneath 1963; Sneath and Sokal 1973). Numerical taxonomic studies were based on the concept of "sampling the phenome", ideally with 60 or more characters from a wide range of body parts of systems to reliably estimate phenetic differences among taxa. The extension of this concept to studies of geographic variation derives in part from the taxonomist's desire to construct intraspecific taxonomic units rather than to describe patterns of variation. For example, in his review of the biometric analysis of

geographic variation, Thorpe (1976: 408) states that "information on the racial affinities of populations may provide a basis for taxonomic judgements using formal (*i.e.* subspecies) or informal nomenclature."

The use of a large number of characters has the attendant difficulty of redundancy of information, but here again related concepts get confused. Highly correlated characters are usually redundant measures, and clearly one should not use (say) 10 slightly different measurements of the height of a plant as characters for study. Where highly correlated characters are obviously part of the same functional complex (see Power 1971 for an example), they convey nearly identical information and only one of them should be used. But when they are not part of the same complex they can all be studied, because very likely they are manifestations of a general principle such as size differentiation.

In practice most students of geographic variation choose to study from 6 to 15 characters, preferring to concentrate their efforts on those that can be measured with high precision. Thus, the 28 characters used by Baker and Moeed (1979) in their studies of morphometric variation were reduced to 14 in subsequent studies to increase the precision of the data (Baker and Moeed 1980; Gibson *et al.* 1984). A similar reduction of the number of characters studied was achieved in the studies of Johnston (1969) and Johnston and Selander (1971). Rather than increase the number of characters studied beyond about 20, it is a far better strategy to concentrate on increasing sample sizes and the number of populations sampled.

4. Non-geographic Variation

Several sources of variation can confound the analysis of geographic variation, principal among which are sexual dimorphism, ontogenetic variation, and temporal variation. In sexually dimorphic species the sexes must be treated separately. The extent of sexual dimorphism may itself vary geographically (Johnston and Selander 1973; Hamilton and Johnston 1978; Thorpe 1975), and it may be possible to pool the sexes in some localities but not others. Where sample sizes are adequate, however, pooling should be avoided because separate analyses of the sexes are valuable "replicates" which may aid in assessing the adaptive significance of geographic variation.

Different ontogenetic stages of a species such as larvae, pupae, adults, or age classes have to be analyzed separately (see Thomas 1968 and Atchley 1971). In species with indeterminate growth and no means of assignment to age cohorts, ontogenetic variation is a particular problem. If ontogenetic variation is primarily size-based, there are two common ways of adjusting the data for the effect of allometric growth before analyzing geographic variation, as follows:

- (1) Adjust an allometric character with its regression slope on a standard size character, using logarithmically transformed data (Gould 1966). The bivariately adjusted characters are then analyzed for geographic variation.
- (2) Adjust the allometric characters by regression against a standard size character, using the pooled within-locality slope (Thorpe 1975, 1976). The pooled-within locality slope is appropriate if there is geographic variation in the allometric characters and if specimens differ in size among localities. The characters are again transformed logarithmically to produce linearity between the allometric and size characters. The adjusted characters can then be ordinated with multivariate statistical techniques such as principal components analysis to display differences among samples (see Thorpe 1976: 414 for an example). Residuals from regression with the standard size character could also be used (Reist 1983), but they are less tractable biologically than the adjusted characters. The use of ratios wherein each character is divided by a standard size measurement is inappropriate here because of the undesirable statistical properties of ratios (Atchley *et al.* 1976).

Temporal variation arising from samples collected in different seasons or years is a contaminant of unknown magnitude in most studies of geographic variation. Where it has been studied, the temporal component has usually been much smaller than that due to geographic variation (*e.g.* Kaesler 1971; Hill 1959; Gould 1969; Rising 1973; Bryant and Turner 1978; Zink 1983). Temporal variation can be eliminated or minimized by sampling in the same season each year and by completing the sampling of localities within the shortest time frame possible.

B. Extent and Pattern of Geographic Variation

1. Differences Among Samples

Most analyses of geographic variation seek to objectively measure differences among samples, to partition the samples into groups on the basis of similarity, and to display the pattern of variation on a map or in some measurement space (Gould and Johnston 1972). Because the degree and pattern of differentiation among localities is heavily dependent on the particular set of localities sampled, the characters chosen for study, and the sample sizes assembled at each locality, the analysis of geographic variation is necessarily quantitative and requires the application of statistical methods. The first step in any study is to describe and statistically evaluate differences among samples, either at the level of individual characters (univariate analysis), or by considering simultaneous variation and covariation in all characters (multivariate analysis).

Before computers became widely available to carry out the heavy computation associated with multivariate statistical analysis, most studies were of relatively few characters considered individually. An excellent example of this approach is the study of Brown (1963) of geographic variation in the head crest and associated facial markings in Steller's Jay (*Cyanocitta stelleri*) (Fig. 1). The lack of concordance among characters was a major frustration of many univariate analyses, often given confusing results in which some characters varied clinally in one direction, others in the reverse direction, and still others in an apparently haphazard way.

The utility of multivariate statistical methods in synthesizing these disparate trends into a coherent view was demonstrated convincingly by Johnston and Selander (1971) in their study of North American

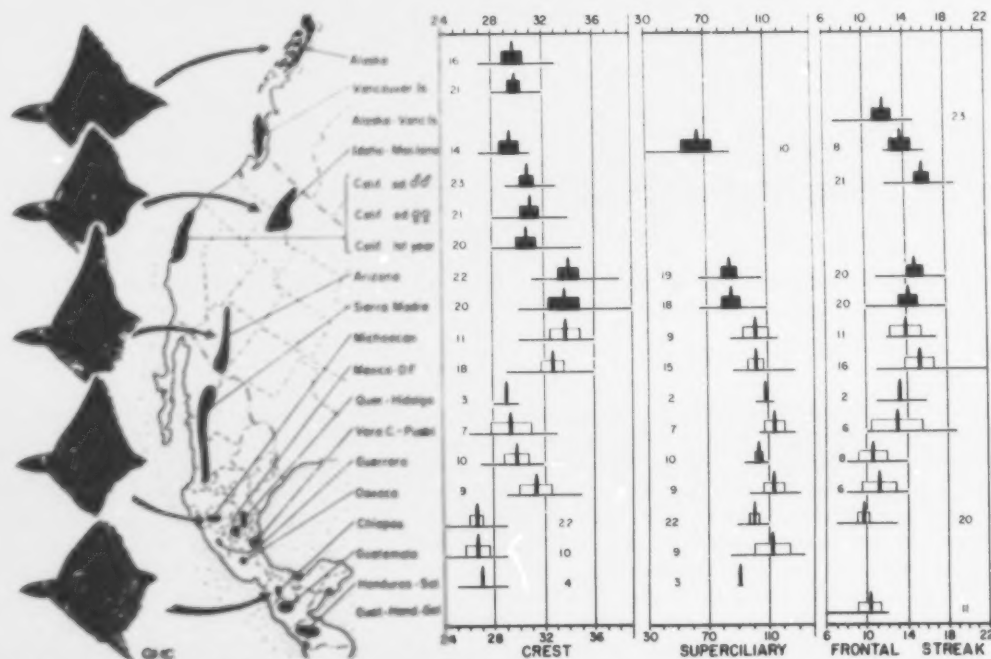


Fig. 1. Geographic variation in crest length, superciliary line length, and frontal streak length in Steller's Jay (*Cyanocitta stelleri*). Each character is expressed as a ratio of wing length. Means, ranges, two times the standard error on either side of the mean, and sample sizes are depicted for each sample. Black-crested samples are represented by black bars, blue-crested samples by open bars. The Michoacan and Mexico-D.F. samples contain birds with black, blue, and intermediate crest colours. (From Brown 1963, Fig. 2)

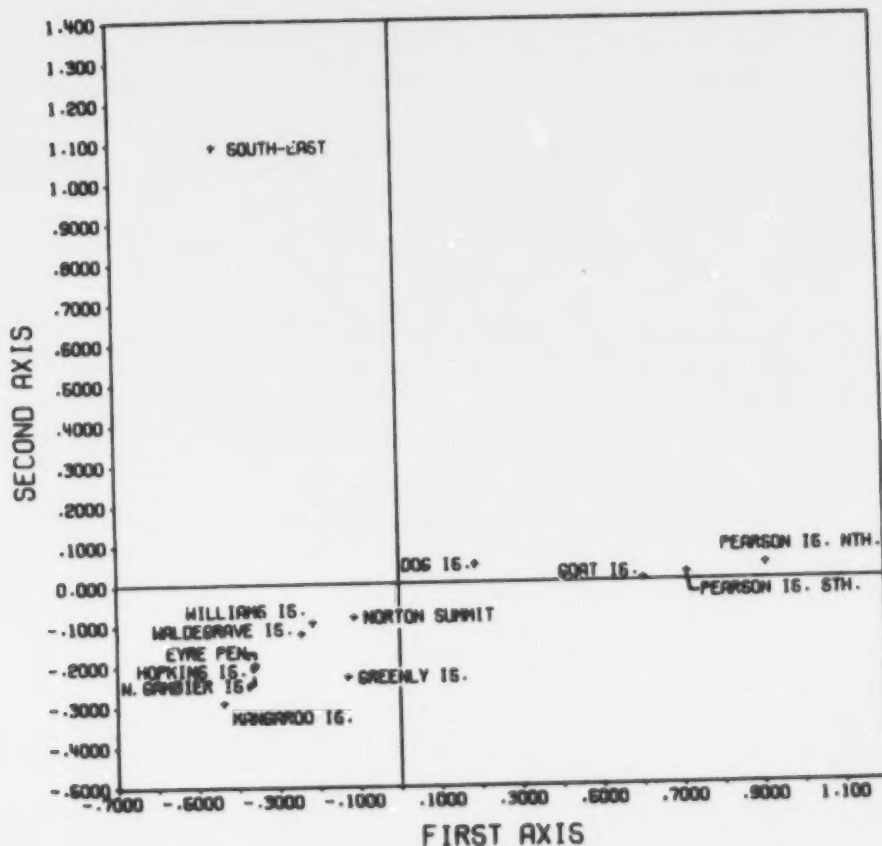


Fig. 2. Geographic variation in gene frequencies of populations of the Australian Bush-rat (*Rattus fuscipes*) as revealed by the first and second axes of a correspondence analysis. Two groups are revealed, one consisting of Goat Island, Pearson Island South, and Pearson Island North, and a second consisting of all other populations except Dog Island and South-East. (From Schmitt 1978, Fig. 4)

populations of House Sparrows (*Passer domesticus*). They used principal components analysis to identify uncorrelated complexes of covariant characters (involving size and shape) which were aligned neatly with different environmental measures. Although these methods are now routinely applied to phenetic characters (see Gould and Johnston 1972; Thorpe 1976), they have also found application in the description of genetic differences among populations. For example, compare the different trends of geographic variation in various polymorphic loci (see Fig. 2 in Schmitt 1978) with the multivariate summarization achieved with correspondence analysis (Fig. 2) in the study of the Australian Bush-rat (*Rattus fuscipes*). The latter analysis distinguishes two groups of isolated populations and two outlying populations which were not obvious from the single-locus allelic distributions.

A popular multivariate technique for the analysis of morphometric data, where the more stringent criteria of multivariate normality and homogeneous variance-covariance matrices are likely to be met, is that of generalized discriminant analysis (Seal 1966; Cooley and Lohnes 1971). The advantage of this approach is twofold: (1) the separation of the locality centroids is maximized; and (2) confidence regions can be superimposed about them to indicate the reliability of their locations. When characters are plotted as vectors in the same space their contributions to the separation of the locality centroids are readily

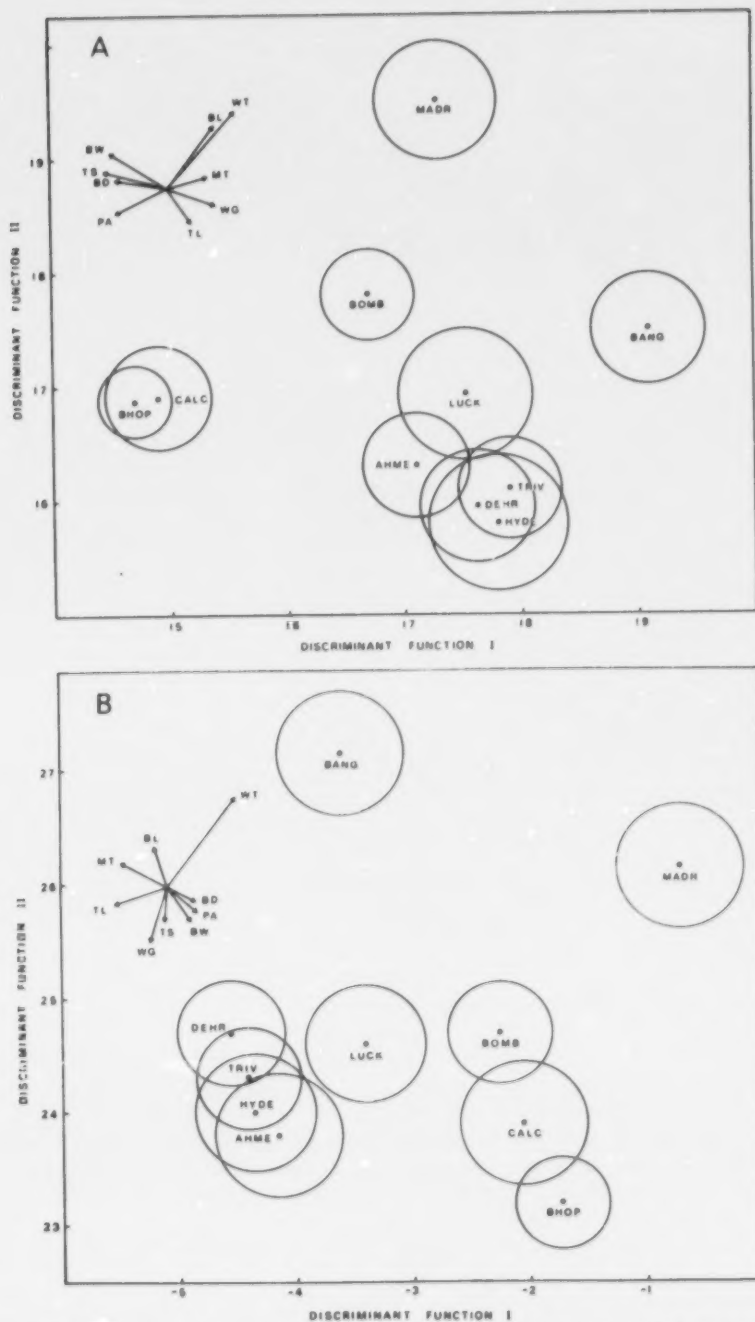


Fig. 3. Bivariate plot of discriminant functions I and II for male Common Mynas (*Acridotheres tristis*) from 10 Indian localities. Locality centroids are enclosed by 95% "confidence circles." Contributions of individual characters to the separation of locality centroids are indicated by the magnitude and direction of the character vectors, which are scaled relative to the pooled within-group standard deviations. Acronyms identify localities as in Baker and Moed (1980). (From Baker and Moed 1980, Fig. 3)

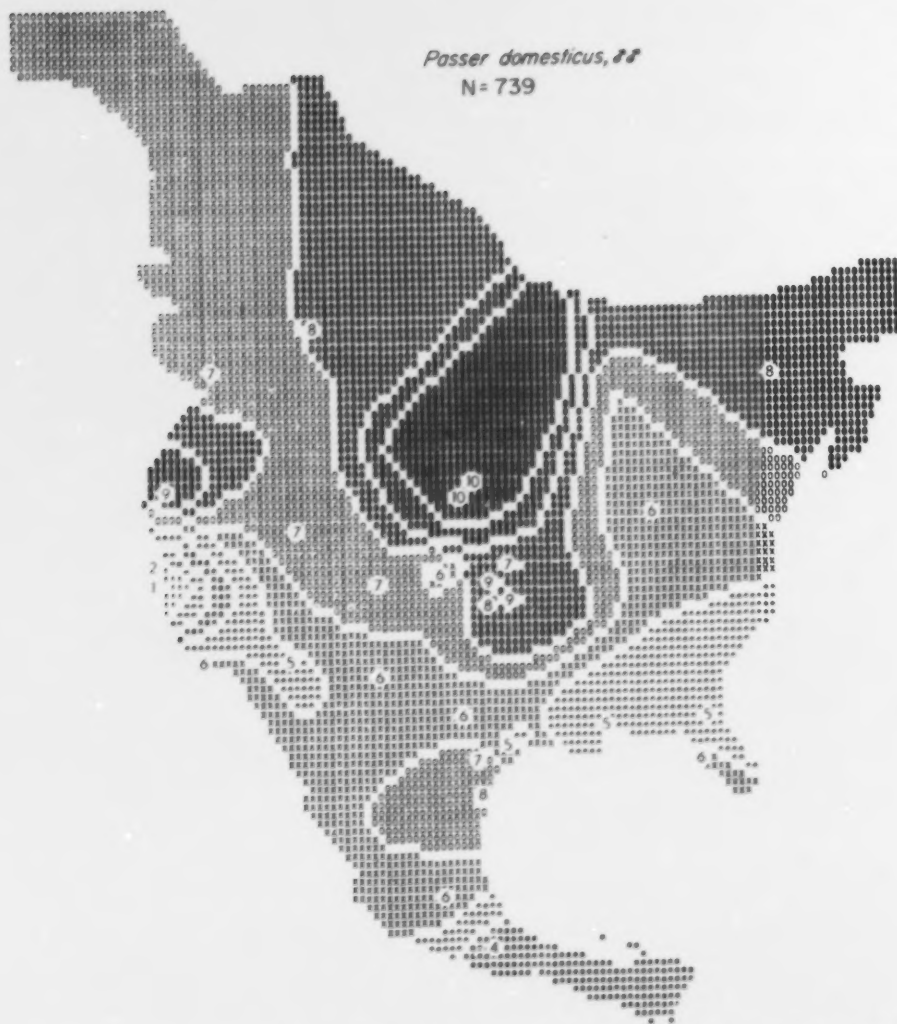


Fig. 4. Contour diagram showing geographic variation in mean principal component I scores of 16 skeletal characters of male House Sparrows (*Passer domesticus*) in North America. "Darker" symbols and higher numbers indicate greater scores (larger "size" as commonly interpreted). (From Johnston and Selander 1971, Fig. 7.)

apparent (Fig. 3) (see Barlow and Power 1970; Power and Tamsitt 1973; Baker *et al.* 1978; Power 1979, 1980; Baker and Moeed 1980).

The establishment of statistically significant differences among population samples raises the more specific question of how much of the total character variance is among local samples, rather than within them. Variances can be partitioned into within- and among-locality components with analysis of variance, as has been done by Sokal and Thomas (1965) in their study of alates and stem mothers of the Gall-making Aphid *Pemphigus populi-transversus*. For some additional examples on diverse data sets see Atchley (1977a & b), Bryant (1977), Bryant and Turner (1978), Johnston (1976), and Baker (1980).

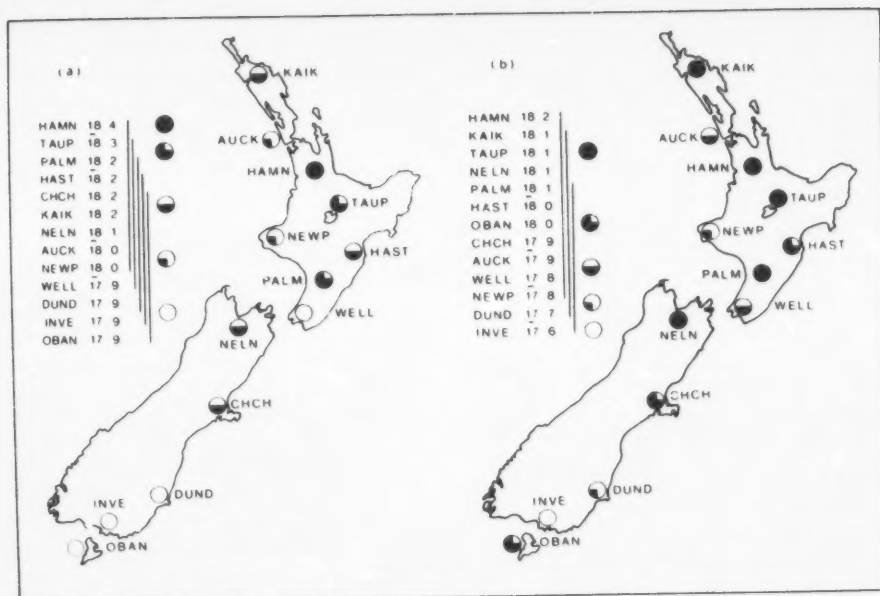


Fig. 5. SS-STP results for humerus length of (a) male and (b) female New Zealand House Sparrows (*Passer domesticus*). Vertical lines define maximally nonsignificant subsets of locality means. Various shaded circles indicate trends in character variation. The character range is divided into five equal parts from largest represented by solid circles through smallest denoted by open circles. For further details see Baker (1980). (From Baker 1980, Fig. 2.)

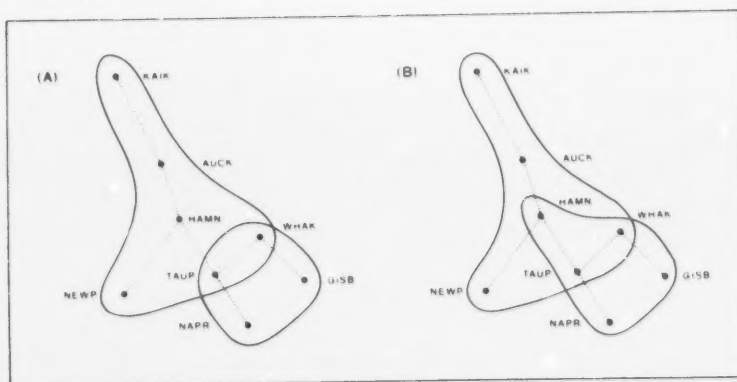
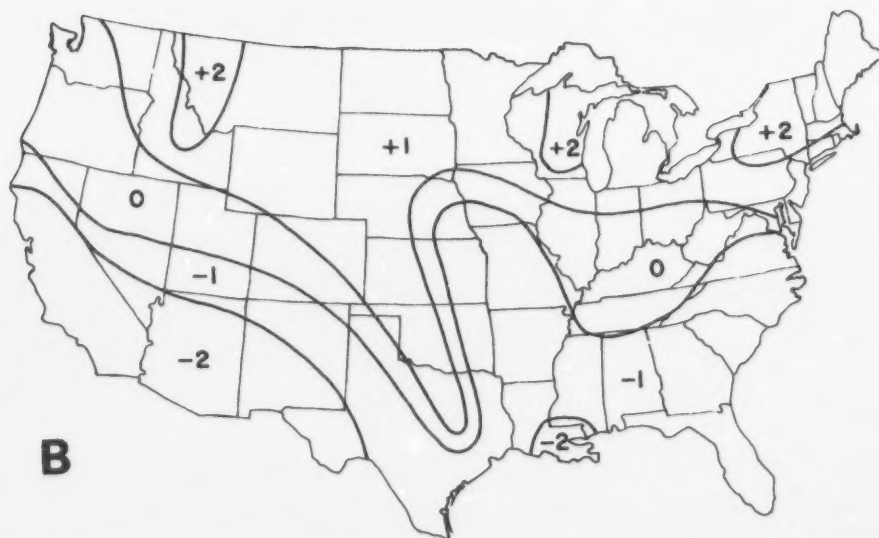


Fig. 6. Maximally acceptable sets of locality centroids defined by MANOVA-STP for (A) males and (B) females of Common Mynas (*Acridotheres tristis*) from eight localities in New Zealand. Contiguity relationships of localities, based on minimal geographic distances, are shown by the dotted lines. The centroids are plotted at their geographic locations rather than their locations in discriminant space. See Baker and Moeed (1979) for further details. (From Baker and Moeed 1979, Fig. 5.)



A



B

Fig. 7. A. Geographically connected sets of locality scores of principal component 1 based on 14 morphometric characters of Houseflies (*Musca domestica*) in North America. Results are averaged over the sexes. Lines connect pairs of localities not significantly different by the protected least significant difference (LSD) criterion. B. Contours of standardized locality scores of principal component 1, averaged over the sexes. (From Bryant 1977, Fig. 1.)

2. Patterns of Variation

The pattern of geographic variation is most conveniently displayed by plotting sample statistics on a map of sample locations. There are two common methods of doing this, referred to as trends and partitions (Gabriel and Sokal 1969). Trends are appropriate for characters that vary continuously across geographic regions, whereas partitions are better applied to the delineation of subregions within which samples are homogeneous. Because trends are smoothed contours interpolated among localities, they are especially sensitive to local sampling errors, and also require a large number and wide distribution of samples to engender confidence in higher order surfaces.

Trends have commonly been presented as univariate contours or "isophenes" (e.g. Marcus and Vandermeer 1966; Vandermeer 1966; Adams and Turner 1970; James 1970), but more sophisticated analyses have contoured multivariate indices on maps. A striking example of this is the computer-generated map of principal component I scores (representing body size) of North American House Sparrows (Fig. 4) in Johnston and Selander (1971). A further refinement incorporates three-dimensional models depicting varying rates of character change among localities as undulations in surface relief, as has been done by Eger (1983) for morphometric variation of Ermine (*Mustela erminea*) populations in North America and by Bishop and Cook (1975) for morph frequencies of the Peppered Moth (*Biston betularia*) and the Scalloped Hazel (*Gonodontis bidentata*) in Great Britain.

Partitioning techniques have been used much more frequently than trends in the analysis of geographic variation, mainly because of their statistical elegance and tractability. A common approach has been to categorize character variation univariately with the sum of squares simultaneous test procedure (SS-STP), an *a posteriori* multiple comparisons test which follows analysis of variance (Gabriel

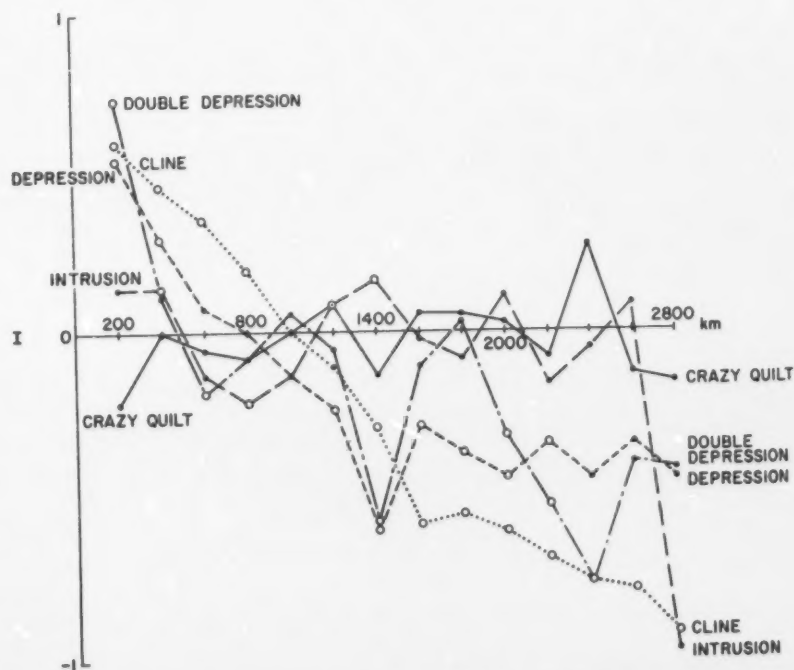


Fig. 8. Correlograms for five artificially generated variables, to simulate distinct patterns of geographic variation. The correlograms are based on the Gabriel network and map in Fig. 7 of Sokal and Oden (1978a). Distance in km between localities is graphed against Moran's autocorrelation coefficients (I). Open circles denote significant autocorrelation coefficients ($P \leq 0.05$). (From Sokal and Oden 1978a, Fig. 8.)

1964). Analyses have been based on ranked means (e.g. Barlow and Power 1970; Johnston 1969; Power 1970; Rising 1970; Johnston and Selander 1971, 1973; Powellson *et al.* 1975; Baker *et al.* 1978; Baker and Moeed 1979, 1980; Baker 1980; see Fig. 5) or on geographic contiguity (e.g. Gabriel and Sokal 1969; Highton 1977). A related technique, the Student-Newman-Keuls (SNK) test, has also been applied successfully to the analysis of patterns of geographic variation in various organisms (e.g. Sokal and Rinkel 1963; Rinkel 1965; Sokal and Thomas 1965; Adams 1970; Ross and Baker 1982).

Multivariate extensions of these techniques (Gabriel 1968) following multivariate analysis of variance have not been widely used, despite their obvious usefulness (e.g. Sokal *et al.* 1971; Baker and Moeed 1979, see Fig. 6). Multivariate indices are also amenable to partitioning techniques, as has been done by Bryant (1977) for populations of the House Fly (*Musca domestica*) in the United States. He partitioned principal component I (representing "body size") using the protected least squared differences (LSD) *a posteriori* test (Carmer and Swanson 1973). Interestingly, the LSD partitions do not fully reveal the clinal nature of variation in this example, which is better depicted by contours (Fig. 7).

The ultimate goal of the above techniques is to reveal the pattern of geographic variation, such as clines, discontinuities, local intrusions, patchwork quilts, *etc.* Recently, tests have been devised to test the significance and departure from randomness of these patterns. Royalty *et al.* (1975) devised a test for ranked data, which has been used to assess patterns in several studies (e.g. Selander and Kaufman 1975; Bryant 1977; Highton 1977; Levin 1977). Application of Mantel's test (Mantel 1967) to geographic variation patterns was pioneered by Sokal (1979), and has subsequently been used successfully by others (e.g. Jones *et al.* 1980; Eger 1983).

The technique of spatial autocorrelation (Cliff and Ord 1973) which tests whether the observed value of a variable at a locality is significantly dependent on its values at neighbouring localities, has been utilized in geographic variation analysis by Sokal and Oden (1978a & b). They extended the technique with spatial correlograms which display autocorrelations with distance between pairs of localities. The correlograms summarize patterns of geographic variation in each character (Fig. 8).

III. EVOLUTIONARY SIGNIFICANCE OF GEOGRAPHIC VARIATION

To assess the evolutionary significance of geographic variation we must go beyond the description of its magnitude and pattern into the realm of causal analysis. Until the causes of microevolutionary processes are better understood it will not be possible to make generalizations of relevance to evolutionary biology and systematics (Barrowclough 1983). Inferences about the cause and evolutionary significance of geographic variation among populations of a species devolve around two basic questions, as follows: (1) is it selectively based and what are the agents of selection, and (2) are differences among populations the raw material for speciation? As we shall see below, both of these questions are extremely difficult to answer objectively and unequivocally.

A. Evidence for Selection by Environmental Agencies

Three lines of evidence have been adduced in support of selection by environmental agencies, as follows: (1) phenetic affinities of samples; (2) patterns of character covariation; and (3) associations of environmental and phenetic variables.

1. Phenetic Affinities of Samples

What can we deduce about the selective basis of geographic variation from phenetic affinities of samples? The majority of analyses of geographic variation in continuously distributed populations show a correspondence between the phenetic similarities of samples and their geographic proximity, and some markedly so (e.g. Jolicoeur 1959; Thomas 1968; Barlow and Power 1970).

While it is tempting to impute selection by common environmental factors as the cause of this correspondence, and to extol the homogenizing effect of gene flow in the absence of barriers to interdemec dispersal, the same pattern could equally well arise by nonselective processes (see Gould and Johnston

1972). The problem with such *ad hoc* invocations of selectionism is simply that we have no way of knowing when they are false. Thus it is equally possible to argue for a selective basis to patterns of phenetic variation in which there is no clear geographic and phenetic conjunction of samples. For example, the geographically discordant nature of variation in the skull of Meadow Voles (*Microtus pennsylvanicus*) has been attributed to strong local selection and "various homeostatic mechanisms" (Snell and Cunnison 1983: 1237). Phenetic affinities of samples are therefore only weak indicators of a possible selective pressure from environmental agencies at best, and most workers seek corroboration from other lines of evidence before hypothesizing ecogeographic adaptation.

2. Character Correlations

The rationale for looking at character correlations as evidence of selection in geographic variation studies is that they represent functional complexes which are presumably linked developmentally and genetically. The persistence of character complexes of highly correlated characters among localities is thought to be more meaningful than that of the constituent individual characters (Gould and Johnston 1972). This supposition seems to stem from the observation that characters related in structure or function tend to be more highly correlated than are others (Berg 1960; Olson and Miller 1958; Cheverud 1982), and this enhanced correlation is due to ontogenetic and selective effects (Van Valen 1965). These effects are based on character correlations within populations, however, and it is not certain how they are involved among populations.

When phenetic variation among samples is factored into multivariate size and shape components, the usual result emerges that samples differ mostly in size. The size factor is a general one involving covariation in all characters, and is a simple consequence of big organisms having big parts and small organisms having small ones. The shape factors usually involve residual variation in some of the characters. Yet geographic variation in size and shape could result solely from environmental induction, with warmer (and more productive) environments generating faster growth rates and larger organisms than cooler ones.

Arguments in favour of a selective basis for among-sample patterns of covariation come from studies involving replicates at various levels of organization such as sex, species, or developmental stage. Johnston (1973), for example, was able to replicate covariant character sets in samples of House Sparrows from North America and Europe, despite the separation of these populations for over 100 years and the distinctive climates they are exposed to in the two continents. He reasoned that natural selection needed to be implicated in the maintenance of this phenetic covariation because the alternative is "enormous unexplained coincidence" (Johnston 1973: 225). Similarly, Baker (1980) replicated these same character complexes in New Zealand populations of House Sparrows introduced from Europe 110 years ago and rejected an ecophenotypic explanation because of the very different environmental regimes there and in Europe.

Although males and females of newly established populations often respond differently to new environments (Johnston and Selander 1971; Baker and Moeed 1979; Baker 1980; Ross and Baker 1982), they nevertheless seem to retain the same patterns of character covariation. Replication of these character complexes between the sexes is probably a general phenomenon because males and females usually show similar patterns of geographic variation, and selection again is implicated as a consequence of their shared genetics.

Similar patterns of character covariation may also occur among different species, reassuring us that the patterns have some generality. For example, Bryant and Turner (1978) compared populations of the Face Fly (*Musca autumnalis*) and House Fly in the United States and found that principal component loadings (defining character complexes) were 86% similar between the sexes and 70% similar between species. Most of the variation in both species involved overall size, and the geographic patterns of size differences were similar for the two species. These results suggest that size differentiation is an adaptive response to environmental selection.

Similar patterns of character covariation have been found in different ontogenetic stages of a species. Female Rabbit Ticks (*Haemaphysalis leporipalustris*) and larval stages have similar patterns of geographic variation, presumably because of similar functional constraints in attachment to hosts and feeding (Thomas 1968). Males differ because of reproductive modifications to their chelicerae and hypostome. Thus an adaptive explanation for these similarities and differences is supported.

3. Associations of Phenetic and Environmental Variables

Because breeding experiments are difficult to carry out either in the laboratory or in the field, the best evidence for environmental selection as the primary agent of geographic variation comes from the expected strong correlation of phenetic and environmental variables (Gould and Johnston 1972). An association of these variables is, in itself, not very compelling evidence of selection because it could be mimicked by nonselective isolation-by-distance. Differentiation between these two hypotheses usually relies on a sound functional explication of the observed phenetic differences as adaptive responses to environmental variation.

Parallel geographic variation in different species and consistent correlations with environmental gradients have long been recognized and formalized in ecogeographic rules (Gloger 1833; Bergmann 1847; Allen 1877). As noted by Rensch (1960), the rules are of limited generality because of conflicting selective pressures from other agencies.

In a study of geographic variation in 12 North American species of birds, James (1970) found a close relationship between wing length (and presumably body size) and wet-bulb temperature, consistent with results of earlier studies by Hamilton (1958, 1961) and Power (1970). This led James to reformulate Bergmann's Rule as follows: "Intraspecific variation in homeotherms is related to a combination of climatic variables that includes temperature and moisture. Small size is associated with hot humid conditions, larger size with cooler or drier conditions" (James 1970: 387). The tendency for birds to have longer wings at higher elevations (Snow 1954; Moreau 1957) is predicted by this reformulation because elevated localities are cooler or drier than their lower counterparts. Climatic selection seems to be implicated as the cause of this pattern of body size variation, but the actual functional mechanism of adaptation is controversial. The conventional explanation is that small relative body surface area in cold climates is a mechanism of heat economy, but this does not compensate for the increased metabolic costs of larger body size (McNab 1971). In reviewing the physiological basis of Bergmann's Rule in birds, Kendeigh (1969) noted that size was only one factor in adaptation to cold. Birds living in northern localities also have increased feather insulation (Kendeigh 1970; Blem 1974, 1981).

The explanatory power of the empirical ecogeographic rules is open to question, especially when they seem to apply in some parts of a species range and not in others. For example, Johnston and Selander (1971) found that body-size variation (principal component 1) in North American House Sparrows conformed with Bergmann's Rule, with larger birds at higher latitudes. They also found that a small body core and relatively long limbs occurred in birds at localities with high ambient temperatures, presumably a thermoregulatory adaptation as predicted by Allen's Rule (protruding body parts of homeotherms are shorter in cooler than warmer climates). This apparent fine-tuning of climatic variation to adaptive morphology led Gould and Johnston (1972: 487) to conclude that "the agency of selection seems unavoidable." But why then is the pattern of size differentiation in ancestral House Sparrow populations in Europe directly the reverse of that in North America (Johnston 1973; Johnston and Selander 1973), and why is it also reversed in introduced populations in New Zealand (Baker 1980)? We can conclude that climatic selection is only one of several factors that could mould patterns of geographic variation in House Sparrow populations.

It is difficult to reconcile the heat conservation explanation of Bergmann's Rule with the observation that some poikilotherms show similar latitudinal trends with weight and temperature (Ray 1960; Lindsey 1966). As pointed out by McNab (1971) these trends cannot be explained by thermoregulatory adaptation via heat conservation because most poikilotherms do not actively maintain a temperature different from that of the environment. This does not necessarily mean that the body size trends in poikilotherms are nonadaptive. Body size in the Rabbit Tick, for example, is larger in colder localities in North America, which Thomas (1968) postulated was an adaptation for storage of larger amounts of fat for hibernation.

In their critique of the role of adaptation in evolutionary biology, Gould and Lewontin (1979) pointed out that selection and adaptation could be decoupled in specific instances. They noted that larger patterns of geographic variation could be both adaptive and purely phenotypic, citing Sweeney and Vannote (1978) who showed that many hemimetabolous aquatic insects reach smaller adult sizes when they grow at nonoptimal temperatures. Gould and Lewontin therefore concluded that correlations between climate and geographic distributions of these insects may simply reflect their phenotypic plasticity rather than genetic adaptation.

The tendency for populations in warm and humid areas to be more heavily pigmented than those in cool and dry areas is referred to as Gloger's Rule. Mayr (1970) restricted this rule to birds and mammals and argued that it cannot be ascribed to substrate cryptic colouration because both arboreal and nocturnal animals conform with the rule. However, Northern Leopard Frogs (*Rana pipiens*) from warm and moist areas have more extensive dark pigmentation than those from cold and dry areas, which Schueler (1982) attributed to increased crypsis. He hypothesized that Gloger's Rule results from greater crypsis of darker animals in the deeper shadows and more luxuriant vegetation of warmer and moister areas, possibly combined with the thermal advantages of dark colouration (see Papageorgis 1975).

B. Evidence for Selection by Ecological Agencies

Evidence for selection by ecological agencies comes from three areas of enquiry: (1) the energetics of procuring food; (2) predator-prey relationships; and (3) competition with sympatric species.

1. Energetics of Procuring Food

In mammalian carnivores, annual evapotranspiration (a measure of total primary productivity) is a good predictor of body size in dry and cold environments (Rosenzweig 1968). Rosenzweig interpreted this fit to mean that body size is limited by food supply in deserts and tundra regions with low productivity.

In arguing against the traditional heat economy explanation for Bergmann's Rule, McNab (1971) pointed out that larger individuals have greater nutritive demands than smaller ones even though food requirements decrease proportionately with body weight. This observation overlooks the positive correlation between body weight and length of time a homeotherm can survive without food (Morrison 1960). Body size in adult whales (*Balaenoptera* spp.) is correlated positively with food supplies during the growing season and inversely with the length of the feeding season (Brodie 1975). Darwin's finches on the small arid (and possibly more climatically variable) islands tend to be larger than their conspecifics on larger islands (Downhower 1976).

Strong seasonality may be a potent selective agent for large body size in Muskrats (*Ondatra zibethicus*) in North America, and may well be of significance for other geographically variable organisms (Boyce 1978). In seasonal periods of food abundance selection should favour individuals with rapid growth to large size, which would enhance survival for subsequent periods of food shortage. Large body size has been postulated to be advantageous when food supplies are low because of the increased capacity for the storage of energy reserves. Conversely, smaller body size would be advantageous when flushes of food occur because reserves can be replenished faster than in larger individuals (Calder 1974; Downhower 1976). Selection for increased body size in years of low food availability following a drought has been recently demonstrated in the Medium Ground Finch (*Geospiza fortis*) because large-beaked birds were best able to crack large, hard seeds available then (Boag and Grant 1981). Others have hypothesized an energetic advantage to larger body size in birds as an increased ability to capture, store and transport energy (Blem 1975; Ketterson and Nolan 1976).

2. Predator-prey Relationships

Rosenzweig (1966) suggested that closely related species of actively hunting carnivores were able to coexist because of differences in body size. Groups of species with similar haunts and hunting strategies were referred to as hunting sets. Size differences in a hunting set of weasels resulted in different degrees of specialization on "mouse-sized foods," with larger weasels taking a greater range of prey sizes. A similar relationship between degree of food specialization and body size has also been found in seed-eating finches on the Galapagos Islands (Abbott *et al.* 1977).

Another example is provided by bill-size variation in the Rufous-collared Sparrow (*Zonotrichia capensis*) in South America. The birds in the tropics have large bills and specialize on fruit and insects, whereas their counterparts in the grasslands in Patagonia utilize their smaller bills to take small grass seeds (Handford 1983).

3. Competition with Sympatric Species

McNab (1971) noted that body size (weight) in most latitudinally widespread mammals in North America does not follow Bergmann's Rule. He attributed conformity with the rule by some carnivores and granivores to body-size changes which track gradients in the size of their prey, which in turn is influenced by the distribution of the prey and of other predators sharing the same prey. The increase of body size in higher latitudes is usually found in small carnivores beyond the northern limit of the larger species in a hunting set, and represents character displacement along a latitudinal gradient of species diversity.

The marked variation in body size in Common Mynas in India, which does not parallel climatic variation, may relate to selection for different food-particle size and interspecific competition with other sturnids in ecologically diverse regions of the subcontinent (Baker and Moeed 1980). Latitudinal size variation in the two Chilean Foxes (*Dusicyon culpaus* and *D. griseus*) suggests a trade-off between habitat and food overlap. Increased habitat overlap south of 33°S appears to be compensated for by larger differences in body size of the foxes and in mean size of their prey (Fuentes and Jaksic 1979).

C. Geographic Variation and Speciation

The modern synthesis extrapolated the process of local adaptation by gradual allelic substitutions directed by natural selection as a paradigm for the origin of species (Gould 1980b). The orthodox allopatric model of speciation championed by Mayr (1942, 1963) emphasized the homogenizing effect of interdemal gene flow in central parts of the species range, and postulated the gradual acquisition of reproductive isolation in peripheral populations effectively isolated from gene flow (recently referred to as peripatric speciation by Mayr 1982).

Newer models of speciation, however, question the efficacy of gene flow among demes as an homogenizing force (see Ehrlich and Raven 1969). For example, the theory of chromosomal speciation features chromosomal alterations as isolating mechanisms in sympatric populations (White 1978; Bush 1975; Carson 1975, 1978; Wilson *et al.* 1975; Bush *et al.* 1977). The founder-flush theory (Carson 1975, 1978) involves small demes, chromosomal changes, and extreme bottlenecks during population crashes as requisites for rapid speciation, and has been simulated experimentally with laboratory populations of *Drosophila pseudoobscura* (Powell 1978).

There now seems little doubt that species do originate by adaptive transformations in geographic isolation, (see Lande 1980; Templeton 1980a & b for theoretical treatments) but this is not an exclusive mechanism of speciation, despite doctrinaire statements to the contrary (see Mayr 1982). Local adaptation of populations is insufficient as a causal mechanism for all speciation events, and this discontinuity has been labelled the Goldschmidt break after Goldschmidt (1940) who clearly distinguished the two processes (Gould 1980b).

D. New Directions

The central question in assessing the adaptive significance of geographic variation and its relevance to a general theory of speciation is what portion of character variation is under genetic control and thus amenable to the action of natural selection? As noted by Gould and Johnston (1972), clines could arise by selection by similar latitudinal gradients in climate, or they could equally well be attributed to a non-selective isolation-by-distance model of differentiation. Recently, several innovative new approaches have been taken to try and unravel these two confounding sources of variation, and promise to revolutionize our thinking about the significance of geographic variation.

First, James (1983) designed transplant experiments to estimate the environmental component of geographic variation in the Red-winged Blackbird (*Agelaius phoeniceus*). She transferred eggs between nests in northern and southern Florida, and from Colorado to Minnesota, and discovered that a significant amount of the variation in nestling development is nongenetic. That is, the transplanted nestlings underwent a shift towards the phenotype of nestlings of the foster populations. Reciprocal transplants between the two Florida populations produced asymmetric changes in phenotypic responses, suggesting that there was geographic variation in the genetic component of character variation.

As James points out, the possibility remains that geographic variation may not be adaptive; it may simply be environmental noise. For example, Berven *et al.* (1979) have shown that clinal variation in morphology and development of the Green Frog (*Rana clamitans*) results mainly from environmental induction. Genetic differences in growth rate among localities are the reverse of the clinally ordered pattern. In other species, however, substantial differences in morphology such as those existing between small and large "subspecies" of the Canada Goose (*Branta canadensis*) appear to have a large genetic component because young raised under controlled conditions retain the phenotypes of their taxon (Lack 1974).

Second, a related approach is to estimate local heritability in individual characters. Some particularly interesting work has been done in birds by rearing young in nests of foster parents from the same locality. Offspring-true parent regressions then give estimates of the proportion of local variation owing to genetic differences (Ricklefs and Peters 1981; Smith and Dhondt 1980; Dhondt 1982). Another approach without switching young has been to test for genotype-environmental associations between the morphology of parents and their offspring in different nesting habitats and in clutches of different sizes (Boag 1983). Heritability of multivariate indices of size and shape have been established in laboratory rats, as well as a direct and correlated response to selection for weight gain in a highly integrated suite of osteometric characters from the skull and jaw (Atchley and Rutledge 1980; Atchley *et al.* 1982).

In summary, future progress in understanding the nature and significance of geographic variation will depend on studies on a wide variety of organisms which partition phenotypic variation into genetic and environmental components. It will be particularly important to ascertain not only the magnitudes of these components within populations but also their patterns of covariation among populations.

IV. STUDIES OF GEOGRAPHIC VARIATION IN MUSEUMS

Natural history museums are repositories for specimens collected to record the diversity of life. Variability of specimens within species taxa, the raw material for studies of geographic variation, necessarily entails the collection and preservation of long series from across the range of these taxa. Thus museums are the rightful home of studies on geographic variation as all workers ultimately require curatorial expertise to catalogue, store, and maintain extensive collections emanating from such activities. The correct documentation and preservation of series of organisms are vital to their future use by other workers, especially where the specimens will serve as a benchmark for longer term studies. The large samples dictated by sophisticated statistical analyses can be properly curated only in major museums which have the skilled staff available to handle them, and to arrange access and loans for interested workers now and in the future.

A. Adequacy of Existing Collections

How adequate are existing collections of organisms in museums for contemporary studies of geographic variation? Most major collections of organisms were made early in this century or even earlier, and therefore did not concentrate on long series from planned sampling programmes, but rather sought to record variations from a great range of sites. Very rarely, therefore, are existing collections of specimens adequate for modern investigations (Zusi 1982). This problem is exacerbated by the nature of traditional collections and by the use of material (e.g. skeletons, stained specimens, alcoholics, tissue samples, chromosome preparations, DNA samples) not previously preserved, or curated only in rare instances.

Three examples will suffice to make a general point about the inadequacy of existing collections for geographic variation studies. In a study of the African Mongoose genus *Crossarchus*, Goldman (1983) was able to locate only 153 adult specimens with skins and skulls in museum collections around the world. Nevertheless, this material was critical in establishing the likely existence of four species where only three were known before. Habitat destruction in West Africa and the difficulty of collecting there now make prospects for confirming the existence of these species rather bleak. A second example highlights a commonplace shortcoming of material collected haphazardly in the past. A large series of 400 Ruffed Grouse (*Bonasa umbellus*) in the Royal Ontario Museum was examined by a researcher interested in studying geographic variation in morphometric characters of adults, but close inspection of the skins revealed that most were immatures of no use for his work. This collection simply reflects the fact that younger grouse

are easier to collect. A third example concerns replicate studies of geographic variation in closely related species where it is important to assess temporal sources of variation by making repeated collections of both at the same sites over two or more years. In their morphometric studies Bryant (1977) and Bryant and Turner (1978) collected 846 Face Flies at 25 localities and 663 House Flies at 20 of these localities in the United States. Comparative material for such specific studies as these are simply unavailable in existing collections except in rare instances (see Zink 1983).

Other sources of variation such as sexual dimorphism and ontogenetic variation dilute sample sizes even further, and we are almost always obliged to collect anew for current work. Even with traditional material such as avian anatomical specimens, about one third of the species of birds of the world are unavailable as skeletons and spirit specimens (Zusi *et al.* 1982). We can conclude that present collections can complement modern studies of geographic variation, but very rarely are they extensive enough to fulfill criteria for statistical analyses.

The collection, preparation, and preservation of large series of specimens from a wide geographic range of populations of a species present formidable problems to the practising curator. Many curators working with vertebrates have chosen to prepare flat skins and to also retain the skeletons, effectively doubling the cataloguing, storage, and maintenance workload. Skeletons pose special problems because they are usually cleaned in bugrooms with colonies of *Dermestes* beetles which have a propensity to infest and destroy pelts, mounts, and storage cases. Current controversy over the advisability of using fumigants to prevent or control insect infestations in collections adds to the problem.

Large series of specimens create bottlenecks in cataloguing operations of museums, requiring the generation of corresponding numbers of labels and cards. The only viable solution to this problem seems to reside in computerization of collection data, but again this is a major undertaking. For example, the collection of 135,000 specimens in the ornithological collection of the Royal Ontario Museum took five years of data entry by two operators and almost \$130,000 in external grant support before computerization was completed. Before commencing further studies of geographic variation curators will have to weigh these costs and to assess their collection priorities.

V. SUMMARY

Geographic variation is essentially a statistical phenomenon because its magnitude and pattern can only be estimated from samples of different populations distributed throughout the range of a species. Reliable estimates of character variation and covariation across geographic regions necessarily entail the collection, preparation, preservation, and cataloguing of large series of specimens from many sampling sites. Thus, from its inception the study of geographic variation has been based in natural history museums, and this tradition will continue for the foreseeable future because they alone have the expertise and facilities to manage the resultant collections.

The adaptive significance of interpopulational variation is still open to question, mainly because *ad hoc* appeals to selectionism cannot usually be distinguished from nonselective models of differentiation. New studies of the heritability of phenotypic characters within and among populations promise to revolutionize our thinking about the evolutionary importance of geographic variation, especially if they continue to uncover an unexpectedly large environmental component. The synthetic theory of evolution, with its emphasis on the gradual divergence of peripherally isolated populations as the mode of speciation, is under attack as an exclusive proposition. The current debate on the sufficiency of this paradigm will undoubtedly stimulate many new and increasingly sophisticated analyses of geographic variation, and we can look forward to exciting contributions from museum researchers around the world.

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7. MUSEUM COLLECTIONS AND PHYTOGEOGRAPHY

A. CIESKA

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I. INTRODUCTION

In this paper I will analyze the role of regional museums (such as the British Columbia Provincial Museum) in phytogeographic research, especially in geographic areas which are poorly explored botanically. British Columbia is an excellent example of such an area. Its vast, inaccessible areas and limited resources, both human and financial, make botanical exploration difficult. In such a situation the most important tasks of a regional museum are basic floristic exploration and building collections. Without exploration and the support of good collections, advances in other areas of botanical research, such as taxonomy or plant ecology, are inhibited. Little progress can be made in these areas without a background in what appear to be more trivial problems, e.g. the distribution of plants.

Phytogeography and its scope are discussed in Section II. The state of our knowledge about British Columbian flora, the phytogeography of British Columbia, and the history of the flora of British Columbia are discussed in Section III. Finally, Section IV deals with the role the regional museum should play in advancing phytogeographic knowledge in British Columbia and areas similar to British Columbia.

II. THE SCOPE OF PHYTOGEOGRAPHY

A. Definition of Phytogeography

The term phytogeography was originally used for the scientific discipline dealing with the study of vegetation and plant communities and their relationships to environmental factors, rather than with various aspects of the geographic distribution of plants. As more detailed studies of vegetation were made, the earlier concept of phytogeography became known as "plant ecology" or "vegetation science," and the term phytogeography was restricted to that branch of science which deals with problems concerning the geographic distribution of plants. Here I use the term phytogeography in this narrower sense. For the definition, history, and general tasks of phytogeography, see Turrill's (1959) excellent review.

B. Two Aspects of Phytogeography

There are two major aspects of phytogeography. One deals with the distribution of certain taxa. The other deals with the floristics of a certain area. Therefore we speak about the phytogeography of a certain species and mean its area of distribution with all its attributes, or we speak about the phytogeography of a certain area and mean all the species occurring in that area. These two aspects are closely related and their relationship is similar to that between R- and Q- mode in the definition of the factorial model (see Cattell 1965). The basic unit of phytogeographic information, the knowledge that a certain taxon occurs at a certain place, is the same for both the phytogeography of a taxon and the phytogeography of an area. Different types of botanists, however, favour one or the other of these two aspects of phytogeography in their work. Plant taxonomists are usually more interested in the distribution of single taxa, and plant ecologists in the phytogeography of a certain area.

C. Use of Phytogeographic Information

Use of phytogeographic information can be manifold. Data on the distribution of single species or groups of related species are important taxonomic tools. For example, the formal distinction between variety and subspecies is based on a phytogeographic criterion (Davis and Heywood 1963). The distributions of subspecies belonging to the same species are different, but may overlap. The varieties of a species, however, are scattered throughout the distribution of that species. Similarly, one can determine the centre of evolution of a certain group by the overlapping maps of distribution of related taxa.

Maps of distribution can show which species have similar distributional patterns and point to phytogeographical connections and possible migrations of plants in the past. Isolated disjunct occurrences of certain taxa indicate the relict character of certain areas.

In the phytogeographic assessment of an area, great attention is often paid to those areas with numerous endemic taxa. Although this is especially important for higher phytogeographic units, called phytochoria by Turrill (1959), it is less important and less applicable for phytogeographic divisions within smaller geographic areas. However, the restricted occurrence of a few endemic taxa within glaciated areas is a good indication that certain regions escaped glaciation. This is probably the case for the Queen Charlotte Islands (Calder and Taylor 1968; Roemer and Ogilvie 1983) and northern Vancouver Island (Ogilvie and Ceska 1984). On the other hand, the single occurrence of an endemic species in an area with a short postglacial history, such as the occurrence of *Limnanthes macounii* in the Victoria area, cannot be explained easily.

With respect to the phytogeography of a certain area, the composition of the flora can give a good indication of the climatic potential of the area and its suitability for agriculture and silviculture, and provide information similar to the system of biogeoclimatic zones that Krajina (1965, 1972) developed for British Columbia. A detailed phytogeographic classification can complement Krajina's system and make it more precise, especially for smaller geographical units.

The invasion of noxious weeds is one of the problems dealt with by phytogeography. Knowing the area of distribution of a plant which has become weedy elsewhere helps to determine the limiting environmental factors and predict how the plant will expand. As far as I know there are no studies of this kind being done in British Columbia in spite of the serious problems that we have with weeds such as Russian

knapweed (*Centaurea repens*), Scotch broom (*Cytisus scoparius*), and Eurasian water milfoil (*Myriophyllum spicatum* s.str.). Histories of various introductions are only available for a few species (see Reed 1977 for *Myriophyllum spicatum*, and Barbour and Rodman 1970 for *Cakile edentula*), and many others are poorly documented.

Introduced weedy species are excellent indicators of climatic conditions and have been used as climatic indicators (cf. Ellenberg 1950) in areas where natural vegetation has been replaced with agricultural fields, or has been strongly influenced by human activities.

With regard to practical applications, it is often necessary to know the distribution of rare and endangered species in order to divert development from biologically sensitive areas. This is an important task for regional museums, where a separate file of rare and endangered species should be kept and continually updated. In British Columbia preliminary work on a list of rare and endangered species was done during the years 1974-78 by a group of botanists led by R.L. Taylor.

III. THE STATE OF PHYTOGEOGRAPHIC KNOWLEDGE OF BRITISH COLUMBIA

A. Main Manuals for British Columbia Flora

British Columbia is one of the largest areas on the North American continent without a good treatment of its flora. It is rather ironic that parts of this large province (948,600 km²) are treated either as "adjacent areas" (Hitchcock *et al.* 1955-1969) or "neighbouring territories" (Hultén 1968). Hitchcock *et al.* (1955-1969) include occasional references to actual collections from British Columbia. Hultén (1968) provides similar information on dot maps which do not extend very far into British Columbia. In other works, Hultén (1967, 1973) discusses in more detail British Columbian occurrences of certain taxa. The only modern treatment of a part of the province's flora is Calder and Taylor's (1968) "Flora of the Queen Charlotte Islands." However, this flora deals with only a small and rather atypical part of British Columbia. The older floras dealing with the southern parts of British Columbia (Henry 1915; Piper and Beattie 1915) are now obsolete.

Several manuals are indispensable for floristic work and the identification of vascular plants in British Columbia. Hultén's (1968) "Flora of Alaska and Neighbouring Territories," although especially pertinent to the northern parts of British Columbia, must be consulted more or less for the whole province. The work by Hitchcock *et al.* (1955-1969) is excellent for southern parts. Porsild and Cody (1980) and Packer (1983) should be consulted in areas of British Columbia which border on the Northwest Territories and Alberta, respectively. Calder and Taylor (1968) have important discussions of plants found on the Queen Charlotte Islands and also treat some related species which grow elsewhere along the British Columbian coast. Finally, Scoggan's (1978-1979) "The Flora of Canada" has interesting data on the distribution of vascular plants based on holdings of the National Museum Herbarium in Ottawa, and Boivin's (1967-1981) "Flora of the Prairie Provinces" contains numerous important notes on plants and botanical collectors in British Columbia. All these manuals taken together are very helpful in identifying vascular plants. Those who are not taxonomists, however, will encounter problems when they try to combine the different taxonomic concepts and nomenclature presented in these manuals.

Several families have been treated in monographs published by the British Columbia Provincial Museum in its Handbook (Szczawinski 1959, 1962; Taylor 1963, 1966a; Hubbard 1969; Taylor 1973, 1974a & b, 1983) and Occasional Paper series (Brayshaw 1976; Douglas 1982). Taylor (1970) dealt with British Columbian pteridophytes in his work on Pacific Northwest ferns and fern allies. Douglas *et al.* (1983) published a bibliography of selected botanical works related to the flora of British Columbia.

Taxonomic and phytogeographic studies in British Columbia have been summarized in checklists of vascular plants (Carter and Newcombe 1921; Taylor 1966b; Taylor and MacBryde 1977). The most recent of these (Taylor and MacBryde 1977) was based mainly on a literature search and herbaria were consulted only occasionally. Thus it missed some taxa which were collected and their specimens deposited in herbaria, but which were not reported in the literature. Boivin's (1966-67) checklist of Canadian plants, although based mostly on herbaria holdings in eastern Canada, is a good source of information on British Columbian flora. The author indicates which species he had seen specimens of, which records are based on literature only, and which records he considers doubtful.

B. Plant Distributions

Schofield (1969) has given us a good phytogeographic assessment of the Pacific Northwest. He lists plants in groups having similar distributional patterns and discusses the representation of these groups in the flora of the Pacific Northwest. The major groups of "geoelements" (as defined by Walter and Straka 1970) for Canadian plants were illustrated by Porsild (1958) and later for western Canada by Packer (1971). Krajina *et al.* (1982) have classified British Columbian trees with respect to their geographic distribution. Krajina is currently preparing a major work which will provide such information for most British Columbian vascular plants (V.J. Krajina, personal communication). There is a wealth of published information on plant distributions. Little (1971, 1976) and Krajina *et al.* (1982) have provided good distributional maps of trees. Distributional maps are also presented in monographs treating specific groups (see Douglas *et al.* 1983) and in the handbooks and occasional papers published by the British Columbia Provincial Museum (see above). Distributional maps are listed in the "Index Holmensis" (Tralau 1969) and Phillips and Stuckey's (1976) index of those found in North American periodicals.

Caution should be applied when interpreting distribution maps, because these maps reflect their authors' knowledge of the plant distributions which in turn is based on the material available to them at the given moment. Some distributional maps are obviously misleading. For instance, the maps in Porsild and Cody (1980) are very incomplete with respect to the distribution of plants in British Columbia.

C. Floristic Divisions

As I have already stated, there is no phytogeographic classification available for British Columbia. Krajina's system of biogeoclimatic zones, based on ecological principles, classifies areas with presumably the same climax ecosystems into twelve zones. We can assume that the highest units of phytogeographic classification would be approximately the same. In detail, however, phytogeographic classification would differ from Krajina's biogeoclimatic system in that it would stress the phytogeographic uniqueness of some areas. It would thus be necessary to differentiate the southeastern part of Vancouver Island, or the Queen Charlotte Islands, on the basis of the high number of Californian elements or endemic species, respectively. It is possible that some attempts to change Krajina's original classification in certain regions (Annas and Coupé 1979; Pojar and Annas 1980) reflect the recognition of the phytogeographic uniqueness of these regions rather than differences in gross ecology.

Relatively complete lists of vascular plants are available only for a few areas of British Columbia. The Queen Charlotte Islands were covered by Calder and Taylor (1968), the Saanich Peninsula by Szczawinski and Harrison (1973), parts of the Gulf Islands by Janszen (1977, 1981), Wells Gray Park by Hämet-Ahti (1965), and the McBride area by Ceska (1979). Equally important are species lists from smaller areas. These include Hardy's lists (1955, 1957) from Forbidden Plateau and Blenkinsop Lake, van Dieren's (1982) from the Somass River estuary, and Porsild's list from Liard Hotsprings (Porsild and Crum 1961). It is difficult to evaluate the intensity of botanical collecting in various parts of British Columbia without having data on herbarium collections computerized. Brayshaw (1976) and Douglas (1982) have made subjective evaluation.

D. Literature on the Evolution of British Columbia Flora

In order to understand phytogeographic patterns in British Columbia we need to know the history of our area, especially that of the Pleistocene and Holocene periods. Deevey (1949) has summarized the general aspects of the Pleistocene history and biogeography. Although the history of our flora has never been dealt with for the whole British Columbia some discussions, such as that of Daubenmire (1975) for eastern Washington and northern Idaho, are pertinent to the southern parts of the British Columbia interior region.

The main geological event having the most dramatic impact on our flora was the last, or Wisconsin glaciation. During that time most of British Columbia was covered with a thick layer of ice (Clague 1981) and was almost void of vegetation. However, there is a strong indication that some areas of British Columbia escaped glaciation (Thorson and Hamilton 1983), and that some coastal areas were at least temporarily unglaciated (Warner *et al.* 1982). Howes (1981) has discussed the extent of nunataks on

north-central Vancouver Island. Some plants were even able to survive in areas that had been glaciated by migrating from one unglaciated area to another and such a species is called *Wanderrelikt* by Walter and Straka (1970: 372). Thus geological evidence about the extent of glaciation in an area often contradicts biogeographic evidence. A good example of this is illustrated in phytogeographic papers from Norway (Nordhagen 1963; Gjaerevoll 1963).

In British Columbia biogeographic data point to the existence of unglaciated areas on the Queen Charlotte Islands (Foster 1965; Calder and Taylor 1968; Roemer and Ogilvie 1983) and northern Vancouver Island (R.J. Hebda 1984; R.T. Ogilvie and A. Ceska, 1984). A relatively high number of the Queen Charlotte endemics on northern Vancouver Island, the occurrence of several taxa endemic to the Olympic Mountains (such as *Aster paucicapitatus*, *Pedicularis bracteosa* var. *atrosanguinea*, *Castilleja parviflora* var. *olympica*) and taxa endemic to Vancouver Island (*Limnanthes macounii* and *Trillium ovatum* f. *hibbersonii*) all suggest the presence of a chain of nunataks as well as the possible existence of ice-free headlands along the west coast of Vancouver Island.

Nunataks and unglaciated areas probably existed along the ridges and eastern slopes of the Rocky Mountains (Ogilvie 1962; Packer 1980). The assemblage of arctic-alpine plants such as *Carex misandra*, *Eriophorum callithrix*, and *Saxifraga flagellaris*, and mosses such as *Encalypta longicolla* and *E. brevicolla*, were used as phytogeographic indicators of such regions by Packer and Vitt (1974). Possibly unglaciated were parts of the mountains on the southern margin of the Wisconsin glaciation, e.g. the Ashnola Mountains, as well as the peaks of some interior mountains, e.g. the Valhalla Ranges (Little 1960).

The thesis that parts of Vancouver Island and the Queen Charlotte Islands were unglaciated is rejected by geologists (Sutherland-Brown and Nasmith 1962; Prest *et al.* 1968; Sutherland-Brown 1968; Prest 1969; Nasmith 1970). Alley and Chatwin (1979) summarized the Late Pleistocene history and geomorphology on southwestern Vancouver Island, gave the elevational limits of the maximal glaciation and discussed the controversial evidence of the glaciation on west coast of southern Vancouver Island. Archaeologists such as Fladmark (1975, 1978, 1979), on the other hand, favour the idea that there were ice-free corridors on the west coast and along the eastern slopes of the Rocky Mountains.

Another important factor in the shaping of the British Columbia flora was the existence of refugia in neighbouring regions. Coniferous forests persisted south of the border. Daubenmire (1975) postulates the existence of a refugium in the Clearwater Valley in central Idaho. This may have played a significant role in the distribution of oceanic plants in the interior. Detling (1968) discussed the role of refugia south of the British Columbia border in the history of our flora. Cody (1971) has dealt with the imprint of refugia in the Yukon and Northwest Territories on the flora of northern regions of British Columbia.

The Bering land bridge, a broad open area which probably connected Asia with North America, had special significance in the distribution of the so-called amphiberian elements in our flora. The existence of such a bridge was proposed by Hultén (1937) and is still the subject of controversial debates (Hopkins 1967; Yurtsev 1968, 1974; Giterman *et al.* 1973; Kontrimavichus 1976; Murray 1981; Hopkins *et al.* 1982; Ritchie 1984). The hypothetical Beringia would have had a mixture of tundra-like vegetation, drier cold short steppe in uplands, large areas of sands with psammophytic vegetation, and some aquatic and wetland vegetation in depressions (Young 1982; Yurtsev 1982). The majority of the amphiberian plants are characteristic of these vegetational formations.

Pollen analyses of peat bogs and lakes give us a good picture of the development of climate and vegetation after the retreat of the glacier. Studies have been undertaken along the coast (Hansen 1940, 1947, 1950; Heusser *et al.* 1954; Heusser 1960, 1965; Hansen 1967; Mathewes 1973a & b, 1979; Mathewes and Rouse 1975; Hicock 1976, 1980; Hebda 1977, 1983a; Hebda and Rouse 1979; Mathewes 1979; Hicock 1980; Hicock *et al.* 1982) and to a lesser extent elsewhere in British Columbia (Hansen 1955; Miller and Anderson 1974; Hebda 1983b).

With regard to the phytogeography of southern British Columbia the hypsithermal interval [the warmest time being about 8000 years ago (Hebda 1983b)] was the most important period of postglacial time. The climate of that era was generally warmer and drier than it is today. This change is not obvious on the coast of British Columbia although, for instance, pollen diagrams from the Queen Charlotte Islands (Heusser 1960) have registered the pollen of Douglas-fir (*Pseudotsuga menziesii*), a tree which did not and does not occur on the Queen Charlotte Islands but had to be more widespread on the mainland. In the rain shadow of the coastal mountains there was a more pronounced change in the vegetation pattern. There are numerous reports of wood charcoal from elevations above the present treeline. This

evidence indicates that the treeline was higher during the hypsithermal period (Mathews 1951; Lowdon and Blake 1968; van Ryswyk 1969, 1971; Lowdon *et al.* 1971; van Ryswyk and Okazaki 1979). In southern British Columbia this interval ended about 5200 years ago (Clague 1981).

The warmer climate of that time permitted the migration of a group of species which at the present have a more southerly distribution. Some of them, such as *Isoetes nuttallii*, *Githopsis specularioides*, *Trifolium depauperatum*, *Callitriche marginata* and *Microseris bigelowii*, are found in California and Oregon. They occur in the Columbia River Gorge in Washington and reappear again on southeastern Vancouver Island.

A small advance of glaciers was recorded in the period between 2400 and 3300 years ago and possibly also one about 1500 years ago (Alley 1976). There have been several minor advances of glaciers from the 15th century to the present time (Porter and Denton 1967; Denton and Karlén 1973). These advances have been marked by an increase in existing mountain glaciers but have had little effect on the plant distributions.

One of the most dramatic changes in British Columbian flora began with the arrival of Europeans in this area about two hundred years ago. This era was marked by the influx of introduced species which now represent about 21 per cent of the total British Columbian flora (Taylor and MacBryde 1977). The increasing human population in some areas of British Columbia, namely the Victoria area and the lower mainland, has caused the destruction of phytogeographically important localities (Hardy 1957).

IV. ROLE OF THE HERBARIUM

A. Museums and Phytogeographic Research

Phytogeographic aspects are interwoven in all the botanical research conducted in regional institutions. No taxonomic study can be done without paying attention to plant distributions. No ecological study can even be started without knowing the floristic composition of the area in question. Basic phytogeographic problems can seldom be solved without the help of paleobotany, geology, human history, *etc.* It is fortunate that these scientific disciplines are usually represented in museums and that there is thus a good possibility for the cooperation of experts from various fields. Another advantage of regional institutions is that their workers are familiar with the geography of the area and the problems that require study.

B. The Specimen Depository

The basic unit of phytogeographic information is the occurrence of a certain species in a certain locality, regardless of whether we are interested in the distribution of the species or the taxa growing in a certain area. *Each occurrence of a taxon in a locality must be documented by a herbarium specimen.* The primary role of herbaria is obvious: they should serve as a depository of specimens documenting the distribution of plants. The actual role of a herbarium, however, is more complex than merely making sure that specimens have labels with sufficient information and are well protected from carpet beetles and similar pests.

C. The Depository of Information Related to the Collections

The information on specimen labels has to be as complete as possible. This is especially important for rare plants and those which occur at their limits of distribution. For these plants a mere specimen is usually a very poor and insufficient piece of information. Labels on such specimens are scrutinized more carefully than those of commonly distributed species. This is even more true of those specimens collected by prolific collectors. For example, many of Macoun's collections of lichens and bryophytes from western Canada were considered mislabelled because the species in question were not found by other collectors. Only after collecting activities increased in the general area were some of the taxa found again (Crum and Snider 1977; Horton and Schofield 1977; Noble 1980).

Collectors' field notes often provide valuable clues to collecting sites. One of the important roles of a herbarium or museum is to secure the field notes and any other documentation related to collecting activities in the area. In my opinion, it would have been more worthwhile to catalogue and edit Macoun's field notes than to re-edit and reprint his autobiography (Macoun 1979). At the beginning of this century one of the most prolific and knowledgeable collectors on Vancouver Island and the Queen Charlotte Islands was Dr. C.F. Newcombe. His notebooks are preserved in the British Columbia Provincial Archives and contain valuable observations on the distribution of plants, their phenology, etc. They were used in the successful rediscovery of *Woodwardia fimbriata*, a specimen of which was in the British Columbia Provincial Museum and labelled only "Saanich Inlet." The same field notes brought our attention to Mt. Tzuhalem, which is near Duncan on southern Vancouver Island. Almost immediately a proposal was put forward to make this area an ecological reserve.

In many cases collectors' notebooks are either missing or only give sketchy information that is insufficient for the re-collecting of plants. C.F. Newcombe's collection of *Abronia umbellata* from Ahousat and W.B. Anderson's collection of *Polystichum californicum* from Texada Island document plants which in British Columbia are known only from a few specimens. We have no idea as to the exact whereabouts or state of these populations.

Sometimes we get a rather distorted picture of a plant's occurrence from the number of available specimens. For example, there are numerous collections of *Abronia umbellata* from Port Angeles on the Olympic Peninsula. A closer examination of the collecting dates, however, shows that the majority of the specimens were found on the same day by various collectors, who obviously went together on a field trip (N. Buckingham, pers. comm.). The precise locality is also awaiting rediscovery.

D. Maintaining Information on Plant Populations

An important role of the regional herbarium is to maintain records on populations of those plants which are rare, endangered by human activities, or otherwise important from a phytogeographic point of view. The Washington Natural Heritage Program has successfully done this in the State of Washington. The registry of rare and endangered plant species which the Committee on the Status of Endangered Wildlife in Canada administers in Canada, or the Ecological Reserves Program in British Columbia, could serve the same purpose. Because of the dynamic character of the data in such a registry, however, it is important to revisit localities and update information periodically.

E. Directing Collecting Activities Within the Region

1. Professional Botanists

Professional botanists are an important source of phytogeographic information. In addition to university workers there are many other professional groups which deal with aspects of applied botany. They include foresters, aquatic biologists, wildlife biologists, and environmental consultants, many of whom work in the private sector. These groups should be encouraged to use museums for scientific support. Although museums are supported by public funds, the practice of giving aid to the private sector is a wise investment. From such cooperation the museum's main gain is scientific information in the form of voucher specimens, etc. On the other hand, the involvement of museums in the design of private studies can help to assure the validity of the results (see Chapter 12). If one considers the fact that most of these studies are done for various government departments, it is clear that public funds spent on museums and used to help the private sector yield good returns.

Field work in poorly accessible areas is usually a costly proposition. Museum staff should share expenses with field workers from other government departments or be invited to go on field trips with private consulting firms in return for their expertise. In many cases the results of complex projects would be better if the collection and assessment of phytogeographic information related to the project were done by museum scientists. Occasionally, museum archaeologists have been invited to participate in environmental projects but museum naturalists, especially botanists, are usually overlooked. Environmental consultants usually do not have sufficient knowledge of the phytogeography of specific areas and cannot give the client the information required for important decisions. For example, when Ducks Unlimited and

the Canadian Wildlife Service undertook projects on Leach Lake in the Creston Flats area, an obvious oversight resulted in the destruction of the only British Columbia locality of *Downingia elegans*.

Collections which are the products of various studies should be deposited in the regional museum. The same is true for species lists resulting from these studies. The Phytogeography and Systematics Section of the Canadian Botanical Association has made an appeal to deposit species lists in the National Museum in Ottawa, where a depository has been established. Regional herbaria should, in similar fashion, care for species lists pertinent to their respective areas.

2. Amateur Botanists

No project mapping species' distributions within a large geographic area can succeed without the cooperation of all the botanists of the area, including the amateurs. Amateur botanists usually know their areas well because they are able to make visits throughout the whole vegetation season. The ambitious program resulting in the "Atlas of the British Flora" (Perring and Walters 1962) used amateur botanists to a large extent and exploited the initiative and energy that is characteristic of these people. Amateur botanists can help to achieve a better understanding of the flora in a given area quickly and without much expense. Regional herbaria should organize local amateur botanists and give them the necessary guidance and support.

3. Collecting In Poorly Known Areas Or Poorly Known Taxa

The problems associated with collections proper are twofold. One is uneven collecting over a geographic area, due to difficult accessibility, etc. The other is uneven collecting of the various taxa. Grasses, sedges, and aquatics are usually not as well represented as other groups. The mobilization of amateur botanists, the concentration of efforts on problematic areas; e.g. the Queen Charlotte Islands (Calder and Taylor 1968), the organization of collecting forays, and specialized field trips with invited specialists, all can help to improve the situation.

F. Creation of a Data Base

The application of a data-base-management system in herbarium collections should be given top priority. Most material in a herbarium is filed taxonomically. If we are interested in the distribution of a certain species, it is easy to get some idea about this distribution just by leafing through the herbarium folders. The mental picture that one can obtain by going through collections is in some ways more up-to-date than that derived from dot maps.

Dot maps with plotted distributions are especially difficult to update in cases in which misidentifications have to be excluded. A data-base-management system, on the other hand, enables the user to display distributional maps of any taxon based on information stored in the system (Kanai 1984). Furthermore, with a data-base-management system one can ask for more complicated maps, such as maps of a group of species, or maps indicating the intensity of collecting within one area of interest.

Whereas information on species distribution is relatively easy to get from herbarium collections, information on what has been collected in a certain area is almost impossible to extract from a collection. Sometimes documentation of the collectors' activities is also needed. This information again, however, is hidden in the collections and its retrieval is almost impossible. All these problems, as well as the mapping of the distributions, can be sufficiently addressed and solved by a good data-base-management system.

The amount of data to be stored and handled by a floristic data-base-management system requires large memory storage devices which in the past were only available on mainframe computers or minicomputers (McAllister 1983; Pinder-Moss 1983). The recent rapid proliferation of microcomputers and attendant development of suitable software, however, are now making microcomputers more suitable for this task. Their advantages are relatively low cost, no computer time charges, "friendly" operation, etc. Both the hardware and software still place limitations on the size of the data bases but information on a medium size herbarium, up to a few hundred thousand specimens, is manageable if the data base is divided into several separate files. Furthermore, if the tendency to develop inexpensive mass storage devices for microcomputers continues, their future use for this task will not pose many problems.

G. Publication of Phytogeographic Information

The publication of phytogeographically important finds is another task for the museum. There is a definite crisis and gap in this process in British Columbia. The most important finds and phytogeographic papers can be published in the *Canadian Journal of Botany*, *Canadian Field-Naturalist* and *Madroño*. *Syesis*, a multidisciplinary journal published by the British Columbia Provincial Museum, occasionally publishes important biological finds. None of these journals, however, publish finds which represent minor, but regionally important extensions. *Watsonia*, in the British Isles, and various local botanical journals scattered through Germany, are examples of what is needed.

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8. MUSEUM COLLECTIONS AND PALEOBIOLOGY

R.J. HEBDA

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Without the establishment of a tradition of museum preservation it is difficult to imagine how a science of paleontology could have emerged

—Rudwick (1972: 12)

I. INTRODUCTION

Paleobiology in the broad sense encompasses the study of ancient life through fossil remains and related extant biota. In its many faces it has been a cornerstone in the development of museums and, in many cases, the driving force (Ostrom and McIntosh 1966; Rudwick 1972). In fact, fossils were major components of the first recognizable museum collections kept by naturalists Conrad Gesner and Johann Kentmann in the sixteenth century (Rudwick 1972).

It is not surprising that fossils have played an important role in the origin of museum collections. Fossils are natural curiosities because they often occur as organized structures in otherwise featureless rocks. They have frozen the complex symmetry of perishable once-living entities into seemingly indestructible objects. Fossils were of religious significance for, to some, they confirmed the occurrence of the flood, whereas to others they posed serious questions concerning biblical accounts. Fossil remains were even assigned aphrodisiac properties in China. Finally, fossils are easily kept because they are durable, requiring little or no curation to maintain them in their original state.

Fossils are more than just objects of collection, for they have fundamental scientific importance as the record of life's origins and evolution. Fossils record the earliest traces of life and its diversely branching and complex progression toward today's biosphere. They are the record of the stages and paths of evolution and, hence, furnish a key to understanding nature. Darwin recognized that fossils were fundamental to the support of his theory of evolution (Rudwick 1972). It was and is, for the most part, in museum collections that the observed record of the succession of life is housed.

Finally, the study of fossils has immense public appeal because it brings together two every-day spheres of human experience and study: the land and the life upon it — geology and biology.

Following the theme of this book, I will highlight the importance of museum collections to paleobiology and paleobiological research. First, I will outline briefly the nature of paleobiology and paleobiological collections, particularly as kept in museums. Then I will discuss the past relationships between museums and the study of fossils, particularly citing instances where fundamental contributions

have been made to understanding our planet and life on it. Next I will discuss the interaction of paleobiology and museums today. I will conclude with a look to the future of paleobiology and the role museum collections may have in the development of this discipline.

This article is a personal view and as such has biases. Much of the discussion focusses on North America and emphasizes Canadian institutions and examples. Section V (Paleobiology and collections: Ancient Greece - 1960) is based on historical treatments of paleontology and subdisciplines (Weller 1960; Colbert 1968; Rudwick 1972; Bretsky 1979; Rudwick 1979; Valentine and Campbell 1979; Andrews 1980). Sections VI (Paleobiology and Collections: 1960 - present) and VII (Paleobiology and Collections: Future) are based on personal observations, discussions with colleagues and a limited survey of literature. The proceedings of the colloquium on the curation of paleontological collections held in Wales in 1979 (Bassett 1979a) were a valuable source of ideas and information.

II. WHAT IS PALEO BIOLOGY?

Paleobiology, as I will use it in this article, is the study of the remains or traces of past organisms, including their structure, conjectured biology based on comparative studies of modern organisms, their taxonomic relationships, their individual and collective ecology, their biochemistry, their evolution, and their relationship to geologic strata. Basically it is the study of organisms and their environments in the dimension of time, and as such is the examination of the "history of natural history." Thus paleobiology encompasses all aspects of the study of fossils and includes vertebrate and invertebrate paleontology (collectively paleozoology), micropaleontology (remains of microscopic organisms), paleobotany (including palynology), paleoecology, evolutionary paleobiology, paleo-biochemistry (or biogeochemistry), biostratigraphy, and others. Paleobiology today is more or less equivalent to paleontology (see Beerbower 1968; Raup and Stanley 1971:x; or see definitions of both in American Geological Institute 1976: 313-14). The term paleontology is out of vogue, perhaps because the chronostratigraphic emphasis in the past has been replaced by an emphasis on biologic aspects of fossils and diverse approaches to their study.

Classic definitions of paleontology have focussed on "fossils in rocks" (Woods 1967) yet Quaternary fossils or "subfossils" are no less remains of ancient life. The same principles and methods apply to their study, although not necessarily to their collection and preservation. Consequently I include Quaternary fossil studies in the discipline of paleobiology.

The scope of paleobiology is immense for it deals with the form and diversity of molecules to macro-organisms, the nature of microenvironments to continental ecosystems, the examination of individuals within a species to phyletic evolution. It also deals with geologic data, such as the stratigraphy and characteristics of sediments, and is intimately connected with geochronology. As a result, paleobiological collections are incredibly diverse and require a great variety of strategies for collection and preservation.

III. PALEO BIOLOGICAL COLLECTIONS

Paleobiological collections are perceived differently from other natural history collections because of their economic importance in geology. This has led to the segregation of fossil specimens according to their intended use, with consequent differences in curatorial practice. Economically applied collections are usually held by government geological surveys or departments of mines and petroleum resources (e.g. Invertebrate Paleontology collections, Geological Survey of Canada; Institute of Geological Sciences collection in Britain: Rushton 1979) or by industries (i.e. micropaleontological collections of oil companies). Universities primarily house research and teaching collections which are, in some cases, treated as museum collections (Rickards 1979; Strachan 1979). Fossils in government institutions and industry are usually well curated, but university collections are poorly curated even though irreplaceable or type specimens may be included (Doughty 1979; Strachan 1979). Museums keep fossils of significance to natural history, such as vertebrate remains, and these are generally well curated. These museum collections are the backbone of research in paleobiology. Finally there are personal collections which are often well documented and maintained, but in some cases are simply accumulations of curious objects and hence are lost to science.

Collections used in the study of paleobiology are of three sorts:

- A. Fossils with or without enclosing matrix
 - actual fossils or fossil traces
 - fossil preparations such as micropaleontological slides, thin sections, glass slides, acetate peels, latex moulds, etc. (see Kummel and Raup 1965)
 - B. Reference or comparative specimens of extant organisms
 - C. Specimen documentation and reference books (as written, photographic, or computer files)
- I will discuss these in order.

A. Fossil Collections

The principal objects of paleobiological study are fossils in collections. Unlike biological organisms, fossils are not easily studied in detail in the field so they must be collected and retained for preparation and examination in the laboratory. In addition fossils are often fragmentary remains of organisms. The nature of collections has changed little since the 17th century when Johann Kentmann assembled his "*Arca Rerum Fossilium*" (ark of fossil objects) which appeared in the first published illustration of a museum of "fossil objects" (Rudwick 1972).

Fossils, whether petrifications (biologic materials replaced by minerals), compressions (flattened biologic remains), impressions (outlines of organisms or parts), or traces (tracks, etc.), are usually part of a rock or "stone" which is stored in a drawer or case on a shelf (Rickards 1979). A number is painted on the specimen or marked on a card attached, providing reference to the provenance and identity of the fossil. Detailed data for each specimen are almost universally kept on cards or sheets (Fig. 1), in files or, more recently, in computer files backed up by card files (Waddington *et al.* 1978; Brunton 1979; Jones 1979; Light 1979). Typical information recorded includes the name of the fossil, date and locality of collection, name of collector, stratigraphic/geochronologic provenance, and reference to any publications in which the material was included (Fig. 1).

British Columbia Provincial Museum Paleontology Collection		Coll. No.	878	Shelf Loc.	N-8
		Species	Calamophyllia suttonensis		
		Phylum	Coelenterata		
		Class/Order	Anthozoa		
		Location	S. side Cowichan Lake, Van. Is.		
		Long./Lat.	Map 92C16 (48°50'N x 128°12'W)		
		Formation	Sutton		
		Age	Triassic		
		Collector	C.F. Newcombe		
		Ident.	R. Kool		
		Coll. Date	1908	Acc. Date	1979

Fig. 1. Data card for a fossil collection showing typical information recorded for each specimen.

Large vertebrate remains are sometimes restored to an articulated state as mounts, either stored or displayed. For extremely large or heavy specimens the use of warehouse shelving, pallets, and forklifts is necessary. Fragments or very small fossils are kept in vials or small boxes. Small fossils such as foraminifer tests, seeds or conodonts are glued to cardboard micropaleontologic slides. Palynomorph or microfossil preparations are mounted in a solid medium such as gelva or enclosed in a viscous medium such as silicone oil (this allows them to be moved around) on glass slides and filed in cabinets (Kummel and Raup 1965). Microfossil residues are kept in vials. Some materials such as fossil wood, bone, or even algal filaments, are best examined and kept as sections of rock glued to glass slides and ground so thin that structures may be studied microscopically by transmitted light. Acetate peels or latex impressions and casts are another component of collections and again are usually stored in drawers.

Cores or bulk samples of rock or sediment constitute a significant proportion of some paleobiologic collections. These are samples of fossil populations or ecosystems from which the specific material for study must be extracted in the laboratory. These kinds of collections present unique problems because of their size and weight. They are usually kept and "curated" in basements or bulk storage facilities. In some cases special environmental conditions are needed — for example, lake sediment or ice cores are frequently kept frozen to preserve biochemical constituents and organisms, as well as the precise arrangement of strata and sedimentary structures.

Fossil collections are organized in a variety and combination of ways. Specimens may be arranged stratigraphically, that is all fossils of a certain age or from a certain stratum are kept together, regardless of their biological affinities. Material may be grouped by locality or region, again without regard to biologic affinity. Collections may be arranged according to biologic affinities or in evolutionary lineages. The University Paleontological Museum in Oslo has arranged its type collection according to date of publication (Brunton 1979). Personal preference and intended use are the guides to organization rather than adherence to a standard system, especially with smaller collections.

Fossil collections differ significantly from most other museum collections because each specimen often takes a long time to prepare. Although retrieving the material from the field may only require moderate effort, extracting and preparing it for study or display requires enormous expenditures of time and money. Dinosaur skeletons may be hewn roughly from rock in a few weeks, but months or even years are required to clean and mount a single skeleton. A typical pollen core can be obtained in a few days, but processing of sediment samples requires several months, and identification and analysis several more. Even petrified mollusc or trilobite remains may require days or weeks of precise preparation to expose critical features.

It is commonly thought that fossil specimens are petrified and hence impervious to damage, but this is not so (Howie 1979). The fine details of soft parts can easily be scratched or rubbed off. Carbonaceous films (compressions) of plant fossils are extremely delicate and often exfoliate upon exposure. Pyritized material is particularly at risk (Howie 1979). Fossil bones frequently exfoliate and break apart because of fluctuations in relative humidity. The glue that holds fragments together tends to fail after long periods. Microfossil mounts dry out. Specimens may suffer considerably during moves, especially when carried out by non-paleontological staff. In many smaller museums the problem of conservation is particularly severe because curatorial staff rarely have the knowledge or equipment for proper conservation.

The majority of fossil specimens are fundamentally different from biological specimens because they represent species that are extinct and cannot be reconstituted. Furthermore, each exposed section, with its constituent fossils, records a time and place distinct from any other exposure. In most cases there are effectively no finite geographic or temporal limits to indicate whether a representative sample of a taxon has been collected. In general, examples of a taxon are very rare to the point that often only a single type specimen from a single locality exists as a representative. In many cases there is never again an opportunity to collect additional material.

B. Comparative Collections

Since the time of Cuvier, the founder of the discipline of comparative anatomy in the early nineteenth century (Rudwick 1972), modern comparative collections have been of great importance to paleobiological research. Zoological or botanical collections in museums suffice for general comparative purposes, but frequently collections of specific structures of organisms, organized into efficiently usable systems, are required. These are typically not part of biologic collections. Paleobotanists, for example,

need reference collections of modern pollen and spores or stem sections. Vertebrate paleontologists need collections of skulls, fish vertebrae, or sharks' teeth. Such collections are not standardized in scope and structure but are often organized for rapid comparisons of structures among related taxa. The practise seems to be to design the collection to suit the immediate application. If the collection is well conceived and documented it can be of great value to subsequent users. However, in many cases, the organization of such a collection exists principally in the mind of its creator, restricting its future value.

C. Data Collections

There are two kinds of data collections. One category includes the information that documents the fossil material itself. Field notebooks, maps, photographs, catalogues, location files, cards, and computer storage devices constitute the substance of this collection. Relevant data are integral parts of fossil collections although they are curated separately. The other category of data collection comprises reference libraries, catalogues (paper or electronic) of other collections, historical material, etc.

Data collections are curated in a method appropriate to the material concerned (e.g. books in libraries, cards in metal files, etc.). Recently, electronic data storage and manipulation systems have evolved. These systems are tailored usually to the users' needs according to individual formats.

IV. ROLE OF PALEOBIOLOGICAL COLLECTIONS

Fossil collections in museums have three broad functions:

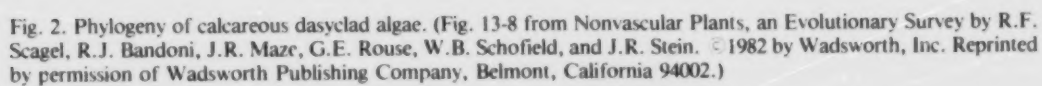
- (a) to house and conserve examples of the record of past life;
- (b) to provide specimens for research; and
- (c) to provide material for display and education programs.

Museum paleontological collections contain, for the record, examples of a particular kind of natural curiosity, fossils. These specimens reveal the nature and diversity of life that existed in the past. Collections are the final reference for identification and naming of entities, especially if they contain type specimens. Exceptionally fine individuals are retained not only for their scientific value but for their natural beauty. Suites of fossils from destroyed or restricted sites are preserved for eventual study. For example, in Canada, access to collect the Burgess Shale localities, which contain delicately preserved Cambrian organisms, is severely restricted by law. This material can only be studied in collections. Historically significant specimens are kept to indicate the basis upon which taxa were analyzed and described, and faunas or floras assembled. Large collections often serve as focal points to attract new material discovered by the public.

Fossil collections are, however, more than just accumulations of interesting or attractive objects. More than for any other science, they are the tangible base upon which all interpretation must be made. Paleobiology is an almost purely historical science and for the most part is based on specimens. This centrality of the fossil collection cannot be overstated for without the collection there would be no paleobiology (Waterston 1979).

The most important research function of collections is to form the basis of descriptive and taxonomic study. Originally described and named specimens either begin or eventually end up as part of museum collections. Future revisions of taxonomic status must be based on these originals. For example, Barnard (1962) described two new species of *Amyelon*, a Paleozoic fossil root genus. In the course of this work he had to examine and emend the diagnosis of thin sections of type material, prepared by Williamson in the late nineteenth century, and kept in the collection of the British Museum (Natural History). The study of North American glyptodonts by Gillette and Ray (1981) shows how museum specimens can be used to describe and classify an extinct group of organisms.

Once identified, specimens are the basis of floras and faunas and can be applied to paleobiogeographic and biostratigraphic compilations. Museum collections are critical to such work because they often contain representative suites from widespread localities and span long time intervals. Collections thus serve as a source for dots on distribution maps and stratigraphic ranges outlined on charts (Hallam 1973, 1977). Many floral and faunal syntheses are based on previously published work (see examples in Ross 1976). However, much of this early research, such as Gregory's (1901) work on echinoid faunas, derives from research directly on museum collections.



Comprehensive faunal and floral studies such as Harington's (1978) synthesis of Canadian and Alaskan Quaternary vertebrate faunas require examination of museum collections. An added advantage of museum collections is that they accumulate material of specific localities from many collectors over a long time. Consequently such collections likely represent the most complete assemblage of taxa from a locality.

Evolutionary lineages can be established from stratigraphically well documented collections. By amalgamating morphologic and provenance data from various collections, it is possible to reconstruct the order of occurrence of related fossils and determine which characters were primitive and which derived.

Hennig (1981) has outlined principles and methods that can be used to reconstruct insect phylogeny from fossil material. Using fossils, he reconstructed the pre-Tertiary phylogenies of most major insect groups. Kukalová-Peck (1983) used fossil specimens to reconstruct the origin and evolution of the insect wing and wing articulation. For easily preserved fossil groups, such as the calcareous dasyclad algae, detailed phylogenies can be derived from fossil collections (Fig. 2).

Morphologic studies coupled with paleoenvironmental data and investigations of modern analogues yield insights into functional morphology. For example, Westermann (1971) studied numerous collections in museums and elsewhere and proposed that complex septal patterns of extinct ammonites were adaptations to withstand implosion by hydrostatic pressure.

Fossil specimens are the only source of "hard" data on the physiology of extinct organisms. Histological studies of compact bone of dinosaurs revealed Haversian-like canals (de Ricqlès 1980). This feature has been interpreted as strong evidence for endothermy in dinosaurs (Ostrom 1980). Dinosaur blood pressures were estimated from heart-to-brain vertical distance measured on mounted specimens (Fig. 3; Ostrom 1980).

Intensive fossil collections from rich sites can yield valuable data on population structure, variability, and disease. The assemblage of canids and felids from Quaternary tar seeps of Rancho La Brea, California, forms an excellent example of such a collection (Stock 1949). In this context, however, the selectivity of the fossil record (Stock 1949; Ostrom 1980; and many others), and the selectivity of fossil collections (Ostrom 1980) must be emphasized. These two filtering phenomena act to bias the population sample and limit interpretation of population biology.

Selectivity is also a serious problem in the use of paleontological collections in the study of paleoecology. Collections made in the past include many individual specimens out of sedimentary context and, hence, out of their paleohabitat. Using these collections, autecological studies are still possible if based on functional morphology; however, synecological investigations usually are not possible. Considerable debate has arisen over the use of dinosaur "census" data (Russell 1967) to estimate predator-prey ratios (Beland and Russell 1980; Farlow 1980; Ostrom 1980). The examples of paleoecological research in Scott and West (1976) clearly indicate that the principle that applies is "study outcrops, not collections." Some museum collections are changing specifically to accommodate paleoecological studies through an emphasis on large sample sizes (Ball 1979).

Microfossil collections, however, can be used to reconstruct paleoenvironments in detail. This is possible because collectors cannot be visually selective, so must take all that occurs in a section of core, or block of rock or sediment. Relative or absolute occurrence of pollen and spore types in a sample are used to reconstruct vegetation and derive climatic and landform history (Figs. 4, 5; Hebda and Rouse 1979; Hebda 1983).

Paleoclimates are derived from collections in other ways (Dorf 1959). In the simplest case, fossil floral or faunal lists or indicator taxa are compared to modern floras and faunas to derive climatic data. This technique is appropriate to estimate general paleoclimatic regimes or relatively recent paleoclimates. Its deficiencies are that identifications must be accurate and that it is assumed that the fossil morpho-taxa lived under the same environmental constraints as their modern relatives. A much better technique is to use the physiognomic features of fossils as climatic indicators (Wolfe 1971). For example, relatively precise paleoclimatic interpretations have been derived from the proportion of entire to non-entire leaf margins in Tertiary leaf assemblages of western North America (Wolfe 1971).

Paleotemperatures can also be estimated from chemical analyses of fossils for oxygen isotope ratios. This technique has been used to infer the temperature of water inhabited by belemnites, an extinct group of cephalopods (Spaeth *et al.* 1971). Oxygen isotope ratios of foraminiferal tests are regularly used to elucidate the relationship between ocean temperatures and glaciations (Shackleton and Kennett 1975).

Estimated Dinosaurian Blood Pressures

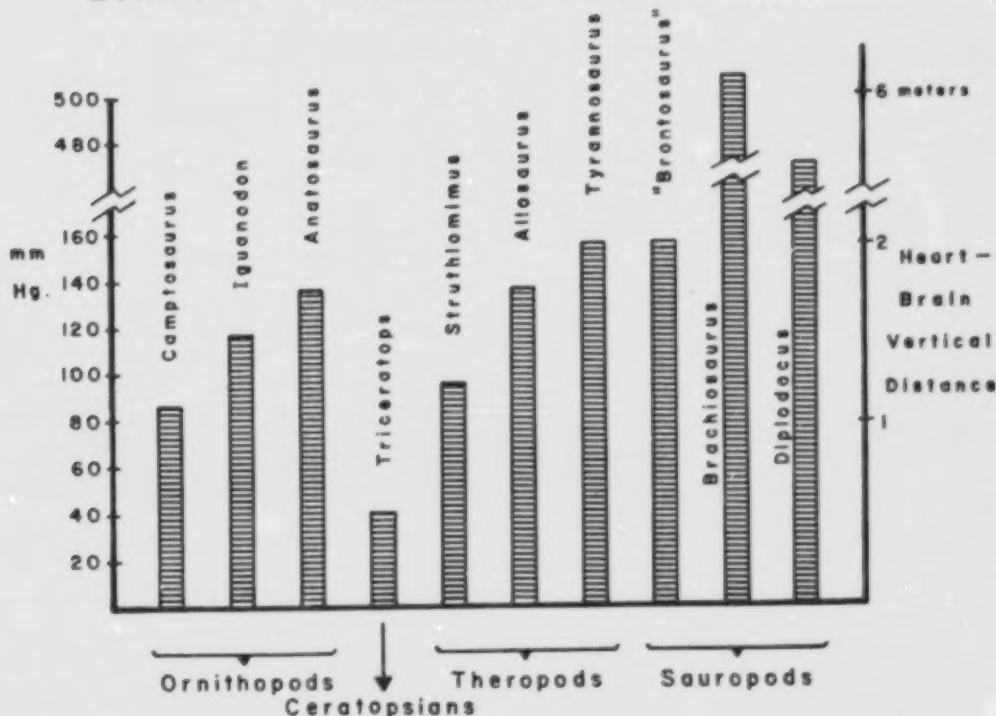


Fig. 3. Estimated blood pressures for various groups of dinosaurs, estimated from heart-brain distances. (From Ostrom 1980, Fig. 6.)

Behaviour is difficult to study from collections because behavioural inferences depend on organism-sediment or interorganismic relationships best seen in exposures (see Chapter 14). However, trace fossils, which are regularly included in fossil collections, provide useful behavioural information. Seilacher (1964) and Frey (1975) outline the principles and applications of using trace fossils for the study of feeding and resting habits, the construction of shelters, sediment preferences, etc. Dinosaur trackways have been used to infer herding behaviour (Ostrom 1980).

Fossil collections generate a need for research on preparation, curation, and conservation. For example, the British Museum (National History) has investigated the role of relative humidity and the deterioration of pyritized specimens and other conservation concerns (Howie 1979).

Finally the basic data derived from research collections are applied to problems in economic geology. Stratigraphic ranges of fossils are used to identify the age of rocks during exploration for hydrocarbons. Paleocological data give clues to environments of deposition which help locate mineral resources.

As educational tools, museum fossil collections are invaluable. Display pieces expose the public to an otherwise technical and specialized science. They not only justify paleobiological research in the public's eye, but reveal to visitors the complexity of life in the past and the dynamic nature of biologic and geologic history. Fossil displays expose the public to the concepts of evolution. They show that some species and major taxonomic groups became extinct and that many others changed drastically. Specimens are used to produce slide shows or films for distribution. Casts are made for smaller museums or travelling displays. Some collections serve as teaching aids in university courses. Specimens provide illustrative matter for books explaining concepts of biology and geology. Such books and displays can also stimulate the interest of future students of paleobiology.

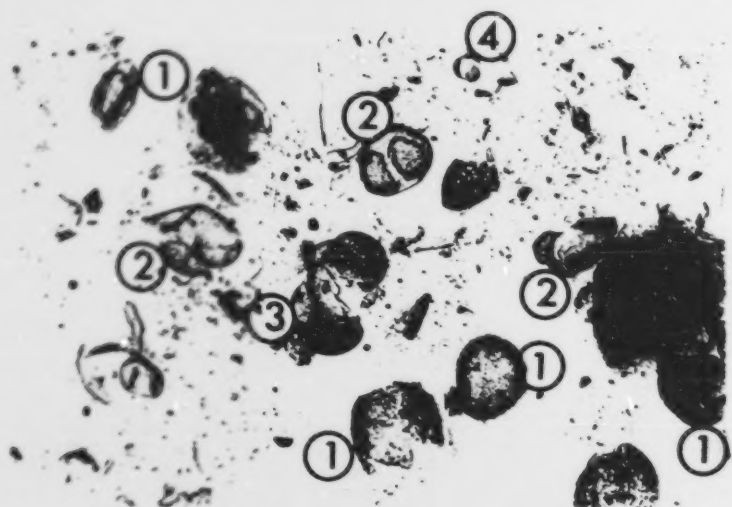


Fig. 4. Example of a typical pollen preparation. Pollen grains of (1) Western Hemlock (*Tsuga heterophylla*), (2) Mountain Hemlock (*T. mertensiana*), (3) Sitka Spruce (*Picea sitchensis*), and (4) Sage (*Artemisia* sp.). Magnification $\times 160$.

V. PALEOBIOLOGY AND COLLECTIONS: ANCIENT GREECE - 1960

Early museum collections grew and were maintained as accumulations of interesting objects, serving as a catalogue of past life. Then during the 19th century they expanded and developed in the context of theoretical progress and controversy. In the first case, specimens were collected, described, and related to each other — basically "classical paleontology" as defined by Weller (1965). In the second case of "explanatory paleontology" (Weller 1965), previous descriptive studies were augmented by new basic work but in the context of addressing theoretical problems usually of a biological nature.

Ancient Greeks recognized and collected fossils, but fossils were almost forgotten until the Renaissance (Weller 1960; Rudwick 1972; Andrews 1980). The first published record of fossil collections or "dug up objects" (fossils in the sixteenth and seventeenth centuries included anything dug up from the earth — Weller 1960) seems to be the book by Gesner published in 1565, "On Fossil Objects" (Weller 1960; Rudwick 1972). Gesner illustrated "fossils" from his own collection and that of Johann Kentmann. This and other publications such as that of Llwyd, which contained the first illustrations of fossil plants (Andrews 1980), were catalogues of fossil objects in personal or institutional "museums" (e.g. Ashmolean Museum, Oxford in the case of Llwyd; Andrews 1980). These accumulations were probably the beginnings of modern museum collections (Rudwick 1972). Fossils were collected and described primarily as natural curiosities, for their biological significance was not understood (Weller 1960).

In the seventeenth and eighteenth centuries fossil objects continued to be collected, described, and illustrated. During this time perceptive work by individuals such as Nicholas Steno showed clearly the organic origin of some fossils (Rudwick 1972). Voyages of exploration and discovery brought back living representatives of fossil groups emphasizing the organic origins of fossils. A profusion of local monographs and treatises was published (e.g. "Herbarium Diluvianum" by Scheuchzer in 1709; Rudwick 1972). Major advances were made in the understanding of rocks and the age of the earth by individuals such as Hutton and Buffon, frequently set, however, in the context of a Biblical flood (Weller 1960).

The foundations of modern paleobiology were laid between about 1790 and 1870 beginning with Cuvier at the National Museum of Natural History in Paris, and ending with the works of Darwin and Huxley. Cuvier established the principles and techniques of comparative anatomy and applied them to fossil remains. His works such as "On the Species of Living and Fossil Elephants" in 1796 made it quite

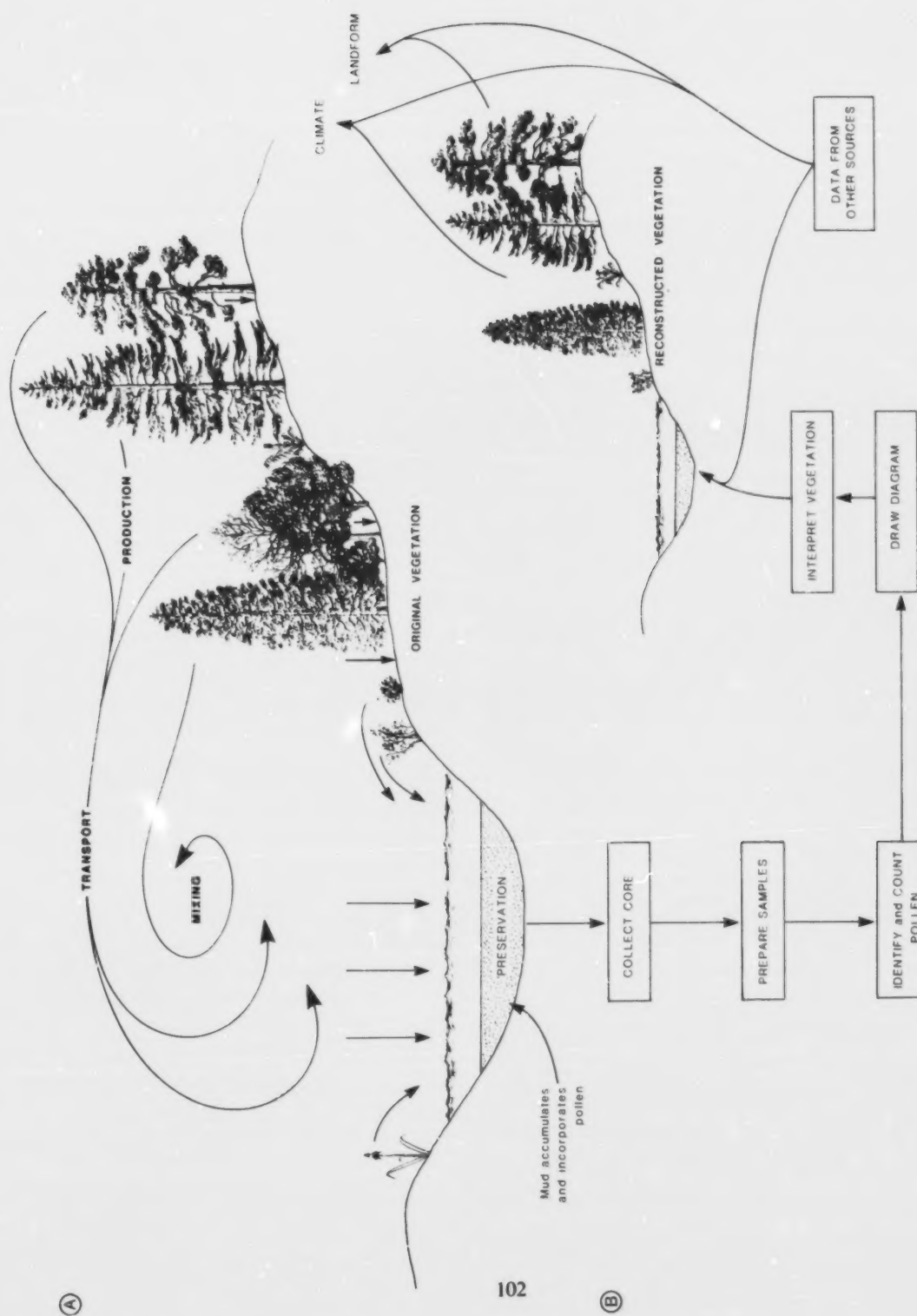


Fig. 5. Formation and interpretation of a pollen assemblage. See Hebda (1981) for further explanation. (From Hebda 1981, Fig. 4.)

clear that many species had become extinct (see Rudwick 1972). Cuvier attempted to explain extinctions on the basis of catastrophic revolutions whereas his colleague at the museum, Lamarck, conceived of species gradually changing into other species. The museum through its publication "Annales du Museum national d'Histoire naturelle," provided a vehicle to circulate the results of investigations (Rudwick 1972). Cuvier with his colleague Alexandre Brongniart studied strata and fossils in the Paris Basin and clearly documented the value of stratigraphic paleontology (Weller 1960; Rudwick 1972), a technique first suggested by William Smith (1815) in England.

By the 1840s England had become the centre of paleontological study primarily because the foundations of modern geology were being developed by men like Lyell. Paleontology became a discipline of great economic significance in mineral exploration. At the same time, the first dinosaurs were recognized and described by Buckland and Mantell (Colbert 1968). The British Museum, recognizing the scientific value of these fossils, paid Mantell £4,000 for his *Iguanodon* collections (Colbert 1968). These strange organisms not only raised critical questions about their origin and nature but stimulated tremendous public interest. By the 1850s life-size restorations were erected in the Crystal Palace through the efforts of Richard Owen, fossil vertebrate expert, Superintendent of the Natural History Division of the British Museum, and principal force in the establishment of the British Museum (Natural History), plus the efforts of Waterhouse-Hawkins (Colbert 1968). Fossil vertebrates had become public-relations vehicles for museums. A division grew between the collections of mundane fossil invertebrates useful in stratigraphy and the collections of extraordinary, large fossil vertebrates.

The work of Cuvier and Lyell, and discoveries of dinosaur fossils, raised serious questions about the origins and history of life. The earth was old; life had been around for a long time. It had been diverse, but many species had disappeared. Life was complex in very old rocks and organisms were apparently well adapted to their environments. There had been a progression of forms: invertebrates - reptiles - mammals; lycopods - gymnosperms - angiosperms. In this setting the evolutionary theories of Darwin and Wallace found fertile ground. Darwin, himself a student and collector of fossils, was aware that the fossil record could provide support for his theories; yet it was woefully incomplete (Rudwick 1972; Bretsky 1979). The search was on for evolutionary sequences and "missing links" for which museum collections supplied raw materials.

The crucial role of museum material in these developments is clearly illustrated by the history of *Archaeopteryx* (summarized from Rudwick 1972). Discovered in 1861 in the Solnhofen quarries of Bavaria, this peculiar fossil was purchased by the British Museum in 1862. Richard Owen published a description of the remains. T.H. Huxley realized from Owen's description that this bird possessed reptilian features. Huxley also recognized that a small bipedal reptile, *Compsognathus*, also from Solnhofen, and described by Andreas Wagner of the Natural History Museum of Munich in 1861, had bird-like anatomical features. Here, Huxley argued, was evidence for the plausibility of the evolutionary theory. The evolutionary model created a framework for fossil collections and a stimulus to collect and describe new types such as the horse series (Simpson 1951; Woodburne and MacFadden 1982).

By the 1880s significant evidence in support of evolution had been found at the intermediate taxonomic levels, but there were only glimmerings of evidence at the species rank, such as the *Micraster* series proposed by Meyer in 1878 (Rudwick 1972). It became apparent that the inadequate fossil record was not going to strongly support evolutionary theory. Without the stimulus of the evolutionary controversy, paleontologists returned to describing fossils, ignoring their biologic and ecologic contexts.

In this setting began an incredible era (1880-1960) of vigorous fossil collecting for museums, the birth of new museums based on fossil dinosaurs, and a return to classical paleontology — highly descriptive, highly publicized, yet theoretically shallow. Rudwick (1972) summarized some of the characteristics of this era: spread of paleontological study to all developed nations of the world, emphasis on applied stratigraphic paleontology accompanied by intellectual narrowing of horizons, exponential growth of descriptive and specialist papers and monographs. Micropaleontology and palynology grew rapidly during this interval. Yet within this increasingly specialized and technical science of paleobiology, fossils, especially fossil dinosaurs, were brought to the man in the street through the medium of museum displays.

The story of early dinosaur collecting, its workers, and its impact on museums and paleontology, is described in numerous publications (Colbert 1961; Ostrom and McIntosh 1966; Colbert 1968; Lanham 1973). In the 1870s the paleontological focus shifted to North America where virgin strata yielded bones of monstrous creatures. The competitive spirit in this pioneering land led to the classic paleontological confrontation between Othniel Charles Marsh, founder of the Peabody Museum of Natural History at

Yale University, and Edward Drinker Cope of Philadelphia. These men collected and wrote tirelessly in a contest of scientific wills. Their adventures led to the discovery of spectacular fossil deposits (Como Bluff, Wyoming; Canyon City, Colorado; Judith River, Montana) and a quantum advance in the knowledge of Mesozoic reptiles and mammals. Their contributions, and those of individuals and institutions that followed, such as the American Museum of Natural History in New York, the Carnegie Museum in Pittsburgh, the Berlin Museum, the Royal Ontario Museum, and the Geological Survey of Canada Museum, revealed an exciting world of huge swamp-dwelling herbivores, armour-plated saurian tanks and flesh-ripping carnivores. Paleobiogeographic knowledge increased through numerous expeditions to new sites in Alberta, Africa, and even Mongolia (Russell 1966; Colbert 1968). Field enterprises spawned new collection and preservation techniques such as the use of the plaster jacket around fossil vertebrate bones. Paleontological specimens became priceless display pieces; every museum needed its own dinosaur (Ostrom and McIntosh 1966).

Dinosaur displays occasionally elicited feedback. After viewing the dinosaurs at the American Museum of Natural History in New York, an Alberta farmer realized that he had seen similar fossils in his area. Thus a new productive fossil locality was discovered.

This era enhanced a niche for departments/divisions of paleontology in many major museums. Museum displays integrated fossil studies because the extinct creatures needed a prehistoric environment thus bringing paleobotanists on the scene. As a footnote, many specimens obtained during the collecting frenzy of the dinosaur era remained unexamined until recently; some still await attention.

The collection of Pleistocene mammalian remains received considerable attention during this time. In North America collectors working in areas such as the Old Crow Basin, Yukon Territory, Canada produced many ice-age vertebrate fossils, most of which are in the collections of the National Museums of Canada (Harrington 1977). The La Brea tar pits revealed a copious and rich deposit of Pleistocene plants and animals, which are now housed mostly at the George C. Page Museum, a branch of the Los Angeles County Museum of Natural History (Stock 1949). The extinct Pleistocene megafauna was of particular interest because some of its numbers coexisted with early man (Martin and Wright 1967) — a fascinating scenario tailor-made for museum presentation.

Paleobotanical studies from 1880 to 1970 also passed through a descriptive, rather specialized phase. Andrews (1980: 133-134), referring to collecting during the early part of the twentieth century, quotes Harris:

“... the proper subject of a fossil botanist's study was to be found in a museum ... or ... specimens sent in by a geologist who wanted to know their age.”

Superb monographs and illustrations of fossil plants were based on collections such as those at the British Museum (Natural History) (Andrews 1980). Curiously, though, most of this work was not done by museum staff but by visiting scientists. The British Museum (Natural History) did, however, recognize its role as a repository and acquired important historical and research collections (Andrews 1980).

Interest in fossils and events of the recent past led to the development of a powerful paleobiological tool — palynology. Scandinavian plant ecologists used the study of microfossils preserved in sediments to decipher wetland history and vegetation change (Faegri and Iversen 1975). Palynology began to be applied to diverse problems, most important from the museum perspective, to deciphering the environments of ancient people. The study of microscopic marine fossils — marine micropaleontology — grew rapidly during the late nineteenth century and early twentieth century (Berggren 1978), but because of its strongly applied character remained largely outside the domain of museums.

The end of the systematic, descriptive era (1880-1960) saw the beginning of the publication of the comprehensive and detailed “Treatise of Invertebrate Paleontology” through the University of Kansas and sponsored by the Paleontological Society of America (Robison and Teichert 1979). Yet even as this monument to classical paleontology emerged, there appeared the first signs that biologically and ecologically oriented paleontology was returning with the publication of the “Treatise on Marine Ecology and Paleoecology Volume 1” (Hedgepeth 1957) and “Volume 2” (Ladd 1957). Significantly there were few museum contributors to the volumes. Museums seemed to be in the conservative backwaters of the approaching paleobiological revolution.

VI. PALEOBIOLOGY AND COLLECTIONS: 1960 - PRESENT

Paleobiology today is in an exciting phase of development. First, major conceptual advances have been made recently such as plate tectonic theory and the theory of punctuated equilibrium (Gould and Eldredge 1977; Windley 1977). In this light, evolution and paleobiogeography are being reconsidered. There is a return to the study of fossil biology (e.g. Bakker 1970; Desmond 1976; Hughes 1976) and fossil ecology (Valentine 1973; Scott and West 1976; McKerrow 1978; Birks and Birks 1980). Principles of physical and engineering theory are being applied to explain morphology and anatomy and infer the behaviour of fossil organisms (e.g. *Pteranodon* flying speed: Bramwell and Whitfield 1970); ammonoid buoyancy and stability (Westermann 1971). New journals such as "Paleobiology" and "Palaeogeography, Palaeoclimatology, Palaeoecology" have arisen to publish this interdisciplinary research (Mantou and Nairn 1965). The basic descriptive and relational work of classical paleontology also continues. The scope of study has broadened through new techniques such as the use of the scanning electron microscope and growth of major subdisciplines such as micropaleontology and paleobiochemistry (Haq and Boersma 1978; Niklas 1980). Second, and probably most important for museum collections, electronic data recording and data communications systems suitable for fossil collections are being implemented. Along with this development, computer modelling is being applied to paleobiological problems (e.g. Gould *et al.* 1977; Solomon *et al.* 1981). Third, the need to protect the paleontological heritage has been recognized and has prompted legislation to conserve some fossil sites (Brideaux 1982).

Collections are still widely distributed among museums, universities, government agencies, and private individuals. Major collections are well organized, catalogued and curated, but are arranged according to a variety of schemes of historical origin, based on researchers' preferences or according to their intended use (Bassett 1979b). There are no universal institutional standards, although subdisciplinary standards appropriate to the nature of the fossil specimen (e.g. plant, calcareous microfossil) are sometimes applied. Many collections in smaller museums, and especially in universities, contain important specimens but are generally in poor condition (Doughty 1979; Strachan 1979). These may be well organized and even well conserved but may have poorly identified specimens. In some cases material is sequestered in boxes or cabinets because of lack of qualified staff to have it properly curated. A growing threat to scientific study is the public fossil market (Gorman 1982; Chatterton 1983). Some high quality specimens of trilobites fetch \$5,000 - \$10,000 each. Fossil fishes and Burgess Shale elements are very much in demand. Many fossil digging leases are being worked in the United States (F. Collier pers. comm.).

A developing concept in the curation of fossil collections is that of collections managers (Bassett 1979b; F. Collier pers. comm.). Collections managers maintain the physical condition and manage the use of the collection. They do not have research as a primary function and so release curators to devote more of their time to research.

The need to exchange information on the nature of paleobiological collections and curatorial techniques has been recognized (Bassett 1979a). An inventory of North American Invertebrate Fossil Collections has been produced (Glenister *et al.* 1977) and a World Directory of Paleontological Collections is nearing completion (Webby 1980; Glenister and Bolton 1983). Catalogues of important collections continue to be published (Bell 1962; Waddington *et al.* 1978; Zedrow and McCandlish 1980; Bolton 1982 and preceding volumes).

Significant public and private funds have been invested in major museum facilities and staff, primarily in response to considerable increases in public awareness and desire for information. For example, a museum completely devoted to paleontology, the Tyrrell Museum of Paleontology, is under construction in Drumheller, Alberta. At the working level of collections in major museums, significant changes are occurring. In most museums, emphasis seems to be on systematizing and analyzing collections made during the golden era of collectors in the early twentieth century rather than amassing new specimens. Much of this work has probably been stimulated by moves to new quarters, needs to use space efficiently and recent cut-backs in funds.

Collections continue to be made, but they focus increasingly on a specific region or on filling in gaps in representative collections, special groups of concern to individual researchers, or sites of extraordinary significance such as Burgess Shale in British Columbia (Collins *et al.* 1983). Fossil and comparative specimens from new categories are being added because of the broadening scope of paleobiology. Good examples of this are fossil fungi at the National Museum of Canada, pollen and spores (Quaternary, pre-Quaternary), and plant macrofossils (Quaternary) at the Royal Ontario Museum, National Museums of

Canada (Jarzen 1977), and British Columbia Provincial Museum. Unfortunately these advances are not reaching into the smaller museums where, because of insufficient staff and funds, fossils continue to be stored in drawers as received, frequently unidentified and essentially uncured.

Technical problems of storage, preparation, and conservation continue. Older collections which have suffered poor curation and management in the past are most affected. Fossil groups are being neglected even in large institutions because there are no funds for specialists to study them. There is a growing conflict of accessibility with controlling access to fossil material because of the exceptional value of certain specimens, or insufficient curatorial staff to oversee use.

Major collections are being put to ever-widening uses. Collections are being re-examined in the light of new paleobiological theories, for example, the "hot-blooded dinosaurs" (see Desmond 1976). Fossils are being analyzed for their paleobiochemical constituents to answer questions of evolution, physiology, and paleoenvironments, and to understand catastrophic extinctions (Niklas 1980; McGowan 1983).

Collections provide the reference materials to evaluate paleobiologic heritage resources, a new and growing concern (Brideaux 1982). Innovative paleobiological displays and educational programs are being designed and constructed which incorporate modern theoretical concepts and modern technology (Chase 1979; Miles and Tout 1979).

Displays and research, based on museum collections, today are integrated efforts involving cooperation of numerous specialists. Holistic reconstructions of past life are emphasized, very much in keeping with the biological and ecological focus of fossil studies. Evolutionary patterns receive attention likely because of new theories and a need to defend paleobiology against the creationist assault.

Museum publications now synthesize current theory and fossils into lively popular versions of past life (Russell 1977; McGowan 1983) or tackle broad questions such as climatic change (Harrington 1979, 1981, 1983) and mass extinctions (Roy and Russell 1976; Russell and Rice 1982). However, some curators feel paleobiology is being overpopularized without a sound research basis. Keys, monographs, bibliographies and catalogues continue to be written (e.g. McAndrews *et al.* 1973; Gillette and Ray 1981; Zedrow and McCandlish 1980).

Because collections data are being transferred to electronic files, detailed inventory and analysis of many fossil collections have been undertaken. Small institutions without access to larger systems such as the Canadian Heritage Information Network have their own data files on local computing facilities.

From the preceding account, it would seem that paleobiology today is in a vigorous state of development. Despite the extremely varied nature of collections and varied research approaches, significant advances are being made and will continue to be made in the "fleshing out" of fossil life.

VII. PALEOBIOLOGY AND COLLECTIONS: FUTURE

In the next few years, progress will depend not only upon fertile research minds and projects, but especially on technical improvements in the handling and management of collections. Soon, for every specimen, it will be possible to obtain accurate, electronic three-dimensional representations to be used with other physical characters and provenance data for comparison with similar material wherever it may be. Wilson's (1983) digitized shark's tooth outlines are a step in this direction. To do this, I suggest we provide money for staff and hardware to develop and apply computer-recording and computer-matching of photographic (or potentially holographic) images, a technique already used by police to identify dental patterns. The most important step in the near future is to inventory and "describe" electronically all fossil material according to a universal standard agreed to by major paleobiological institutions. Standardization is necessary if we are to avoid the development of a plethora of mutually incompatible systems. Such advances could bring the potential for almost instantaneous order in collections.

All significant collections should be recorded, be they in museums, universities, government institutions or private hands. This would begin the resolution of what I perceive to be the most serious problem concerning fossil collections, that of inconsistent and highly variable standards of curation. The analytical capability of computer systems will create the opportunity for substantial advances in paleobiological practice and theory. Most important, "collections" in their electronic form will be available to any fertile mind that wants to use them and, to some extent, also solve the conflict of accessibility with security.

Ideally, collections managers should be hired to oversee all large collections. The principal role of many curators today is to carry out research on collections and transmit the results to the public. These are full-time occupations because curators have enough challenge meeting new technologies and concepts in research. A curator's time often does not allow for the everyday management of the collections even with technical assistance. Collections managers could, first, ensure a high standard of care of the collection. Second, they could concentrate on developing better management techniques.

As pointed out earlier, a long and tedious process is involved in preparation of paleobiological specimens. Unless there is a major increase in the number of preparators, significant advances must be made in the techniques of specimen preparation. The preparation process can cause the greatest delays. Possibly some specimens could be handled in bulk rather than individually. Improved conservation techniques are also needed, not only to preserve irreplaceable specimens but also to decrease the staff time devoted to maintenance.

Collections will continue to increase in volume. Ecological, biostratigraphic, and statistical research will generate large volumes of material. The wide-ranging construction activities of mankind will expose new finds and necessitate the preservation of material from important localities doomed by the bulldozer. Important private collections will continue to be donated to museums. It may be necessary for larger museums to take over significant university collections to ensure that these are not lost. Whatever the source of new material will be, there will be a limit to how much of the earth we can store in buildings. Dale Russell (pers. comm.) has suggested, and I agree, that it will be necessary to practice quality control. If the specimen is of questionable value it will have to be de-accessioned.

There may be a new role for collections in home education. If trends toward individualized learning and increased public awareness continue there will be a demand for visual images for audio-visual programs and casts of specimens for study.

Future research trends seem relatively well defined. Collections will continue to be applied to understanding the processes and rates of evolution by testing hypotheses such as punctuated equilibrium. Fossils must ultimately be used to establish phylogenies and phylogenetic classifications, for despite the speculations based on extant organisms, only fossils record the actual path of evolution. Biochemical, comparative anatomical, and morphological studies of specimens will reveal much of the biology of past organisms. Fossil physiology may continue to be a fertile field. These studies will have to be coupled with work on modern and fossil ecosystems and be related to studies of taphonomy (the formation of death assemblages; see Muller 1979). Collections should continue to form a sound basis for computer modelling experiments. Results of future research may not only shed light on biological phenomena but may also clarify our understanding of the earth and its landforms (especially *vis à vis* uniformitarianism vs. catastrophism) and possibly reveal the nature and frequency of extraterrestrial events (cf. Russell 1977).

Most curators I have interviewed recently emphasize one important point: we will have to get much more information from each fossil to discover the details of past life. In the future, much more emphasis will have to be placed on direct study of fossils. The paleobiological revolution of the last 20 years has often ignored the specimens themselves, but rather it has focussed on previously published lists and syntheses to test and propose new theories. Kuklaova-Peck's (1983) study of the evolution of the wing in insects demonstrates that many years of patient observation and experience with fossil material are necessary to understand correctly fossil structures. If we can apply new techniques such as scanning-electron microscopy and paleobiochemical tests to fossils, we should be able to improve on the work of our predecessors.

In this context I would like to emphasize the need to deposit paleovoucher specimens in museums. Many fossil lists are published and many microfossil assemblages are reported. Yet there is no requirement that the substantiating fossil material be deposited for re-examination. Strachan (1979) suggests that one specimen of each taxon be deposited. Similarly, I would add that one slide of each microfossil sample be deposited. Although these procedures could substantially expand collections, they would allow restudy and verification of previous material, especially if new techniques or theories arise.

A trend that must continue is to study all aspects of fossil sites and to integrate geologic data with the record of all fossil constituents and their physical and chemical remains. These will yield holistic environmental reconstructions and emphasize not only the systematic and life aspects of past organisms, but also their role and evolution in relation to biotic and physical factors. Such work also will help reveal the climatic and physical history of the earth. To achieve these goals, museums will need to broaden collections and research to include the less spectacular, but often more informative, microfossils.

I suggest that more research be done on Pleistocene and Recent deposits. The fossils from these strata usually are least damaged by diagenetic processes. Many of the organisms have closely related living relatives. Chronology can be determined relatively precisely and might possibly be related to numbers of generations. Environmental catastrophes have occurred during this unstable interval leading to mass extinctions (Martin and Wright 1967) and doubtless producing widespread genetic upheaval (cf. Hebda 1983). The life and events recorded in Quaternary strata, because they are less obscured by diagenesis and evolution, should be much easier to interpret in terms of modern processes. The understanding gained from these recent fossils will improve the interpretations for older deposits as well as the nature of modern biota.

If paleobiological work proceeds in the directions outlined, fossil collections will fulfill what may be their most important future function — prediction — whereby the past will be a key to the present and future.

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9. MUSEUM COLLECTIONS, COMPARATIVE ANATOMY AND THE STUDY OF PHYLOGENY

R.J. RAIKOW

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I. INTRODUCTION

The study of vertebrate phylogeny through comparative anatomy would be almost impossible without museum collections. Only they can usually provide the required material, as few people can undertake extended collecting expeditions. Hence the accumulation of a diversity of specimens must be centralized in a small number of large collections to which many people can contribute over time.

This paper will not review either the history of phylogenetic studies or the endless philosophical and methodological debates that enliven the discipline. Instead, adhering to the theme of the present volume, I will focus on the role that museum collections play in these studies, rather than on the studies themselves. To this end I will offer some practical information for those who use museum collections of anatomical (*i.e.* alcoholic or skeletal) specimens, and those who curate them. In addition I will discuss certain matters pertaining to the growth and management of these collections. The opinions and examples given derive from my personal experiences in the study of avian phylogeny, but it is hoped that they will be of more general interest to anatomical systematists.

II. USING ANATOMICAL COLLECTIONS

A. Choice of Species to Study

The primary criterion is relevance to the goals of the project, but it is sometimes possible to choose between two or more equally suitable species. Other things being equal, it may be best to choose the species that is most numerous in collections, so as not to reduce the variety available to other workers. Ease of replacement, however, may be more important than immediate availability. If a museum has two specimens of a rare South American species, and only one of a common local form, then the latter is the obvious choice.

B. Finding Sources of Preserved Specimens

How can one find specimens of a desired group? Anderson *et al.* (1963) listed mammal collections in North American museums. Banks *et al.* (1973) and Clench *et al.* (1976) provided similar information about birds. Some museums have published lists of their holdings (e.g. Ames and Stickney 1968; Blandamer and Burton 1979; Gillette and Bartle 1982).

Many museums can provide printed or photocopied lists of holdings, which are more apt to be kept up to date than formally published lists. In general, starting with such papers, one may write directly to the curators at various museums and tell them what one needs. This system is inefficient, but computerized data banks are beginning to serve as centralized information sources. Inventories of avian skeletal and spirit collections in numerous museums have now been published as bound computer printouts readily available to interested investigators (Wood *et al.* 1982a,b; Zusi *et al.* 1982). These should be invaluable in the short run by helping investigators to find sources of specimens efficiently. However, the information in an inventory is only as accurate as that provided to the compilers. The catalogues in some museums are not up to date or contain errors, and specimens may exist that are not on record. In the long run such inventories will also aid in planning research, as it will be easy to determine whether material is available for a proposed investigation. Inventories will also help museums to plan their collecting so as to fill in gaps. Workers on other taxonomic groups will no doubt produce similar inventories in the near future.

C. Procurement of New Anatomical Specimens

Avian anatomists have long been hampered by the habit of collectors making study skins of the good specimens and anatomical specimens of the rest. Often spirit specimens are found upon dissection to have been sufficiently decayed before preservation or to be so damaged by shot (or, e.g. impact with an automobile) as to be useless for study. The best preserved parts of such specimens are often the maggots. In general, if a specimen is too decayed to make a good skin it can only be saved as a skeleton. If it is too damaged by force (e.g. shot or concussion) to be made into a skin, it is equally useless for spirit or skeletal preparation.

Museums often obtain specimens from zoos, aviaries, or private menageries. These generally lack age or locality data and may therefore be worthless for geographic or alpha-taxonomic work, yet they are perfectly good for many anatomical and phylogenetic studies. Museums should arrange with local institutions to salvage such specimens, stressing the necessity of freezing them as soon as possible after death to prevent decay. This source of specimens is extremely important since such salvage may be the only opportunity to obtain material of rare and endangered species or species found only in distant places. A sometimes unrecognized danger of captive specimens, however, is that they may be ill for some time before death. In this case they may not feed and their muscles and other organs may become emaciated, giving a false impression of their structure to the unsuspecting investigator. In extreme cases the experienced anatomist will usually recognize this condition by the absence of fat, the protruding joints, and the general departure from expected bodily proportions.

D. Preparation and Storage of Anatomical Specimens

For proper dissection specimens should be correctly fixed and preserved. *Fixation* is the treatment of the specimen with chemicals that harden the tissues and prevent their destruction by decay or autocatalytic processes. Unfortunately, the recognition of the need for proper initial fixation is a relatively recent development. Many specimens from the late nineteenth or early twentieth century were simply immersed in alcohol after being collected. Tissues in alcohol-fixed specimens tend to be soft and mushy, muscles pull apart easily, and it is difficult to do a clean, clear dissection. Sadly, many specimens of rare or recently extinct species are available only in this form.

It is not enough merely to place a specimen in fixative. Tissue degradation begins almost immediately after death, and the quality of the specimen will depend on the time needed for the fixative to reach a given area. Feathers and fur impede the penetration of fluid. To avoid this problem fixative (usually a 10% formalin solution) should be perfused through the circulatory system and injected into the body

cavities before the specimen is immersed. If perfusion is not practical, the fixative should be injected into the body cavity and larger muscles, at least. After suitable fixation, specimens are usually washed thoroughly and stored in alcohol; preservation in formalin hardens the tissues excessively. Detailed preservation procedures are found in Berger (1955) for birds, in Quay (1974) for mammals, and in Hildebrand (1968) for all vertebrates.

The position of the specimen during fixation and storage and the size and shape of the storage container can greatly affect the utility of a specimen. If a specimen is jammed into a tight container the mere removal may damage the tissues. It is common to find that in such birds as waders the long, slender tarsi are broken, which makes dissection of the fine tendons and tiny muscles extremely difficult. This is often the result of forcing the specimen into a jar that is too small. If a specimen is fixed in an odd position, the relationships of the structures to be dissected may be very difficult to determine.

The preparation and storage of skeletons is much more straightforward, but partially articulated specimens are useful in a wider range of studies than the completely disarticulated skeletons favoured by paleontologists. Particularly important are the bones of the skull, the sequence of the vertebrae (often preserved by running a string or wire through the vertebral canal), and the thoracic superstructure. Once a specimen has been disarticulated, precise relationships between bones may be very difficult to ascertain. As with alcoholic specimens this problem can be partially alleviated by disarticulating only one side of the specimen. Berger (1955) details the need for articulated skeletons. He also argues against the policy of bleaching skeletons for the sake of appearance as the process erodes the bone surface, destroying fine details.

E. Consumption and Conservation of Anatomical Specimens

In contrast to skeletal materials, which are essentially permanent and reusable, spirit specimens must be dissected, and are gradually destroyed in the process. Nevertheless, a spirit specimen may contribute to many different studies because each worker usually concentrates on a particular part, and the rest of the specimen remains available to other workers, especially if dissection is limited to one side of the body. Investigators studying one part of a specimen should keep in mind the potential contribution of other regions to their colleagues' work, and should try to avoid unnecessary destruction. With rare or unique specimens it is important that various regions be dissected in a sequence that will maximize information retrieval. In the case of a particularly important specimen a group of workers may organize a sequential series of dissections. Subsequent publication of the various papers in one place will then make a significant contribution to the literature.

F. Sample Sizes

The number of specimens used per taxon in a given study is dependent on the amount of variation in the characters used and the level at which this variation is expressed. For phylogenetic studies characters are usually chosen that exhibit low intra-taxon variation but high inter-taxon variation (taxon here refers to the lowest taxonomic unit considered in the study). Practical considerations often dictate how many specimens are used: availability of specimens provides one limit, but for studies involving dissection of soft parts the amount of time that must be spent on each specimen imposes further limits. In studies using skeletal material, the number and complexity of the characters measured or coded may impose similar limits of time. However, the level of intra-taxon variation must be established for each characteristic to be used. Considerable insight can often be obtained from previous experience or from the literature. The examination of a relatively large series for one or a few taxa may be sufficient to demonstrate the normal variation particularly if known sources of variation such as age and sex classes are included.

Developmental anomalies are a potential source of confusion. If only one specimen is studied, how can one distinguish them from normal but unusual species characteristics? The problem may be complicated because a condition normal in one species may appear as an anomaly in another. The only solution is to be suspicious of unexpected variants. I once read a paper (Berlin 1963) that referred to the ambiens muscle in a Common Myna (*Acridotheres tristis*). My attention was caught not only because this muscle has always been considered absent in passerine birds, but because the author did not comment on the unexpectedness of the observation. Suspecting a misidentification I dissected a specimen of the same species and found, as expected, that there was no ambiens (Raikow 1973). To my astonishment, however,

I found another muscle supposedly lacking in passerines, the iliofemoralis externus. Through the kind assistance of A.J. Berger, I obtained and dissected six more specimens from the same local population, and found the muscle absent. Thus the condition could be considered a developmental anomaly, probably representing the reappearance of a muscle previously lost.

Subsequent studies have shown further examples of such apparently atavistic anomalies (e.g. Raikow 1975), other cases suggesting the reestablishment of formerly lost muscles (Raikow *et al.* 1979), and additional cases where the lack of a series did not permit a choice between these hypotheses (Raikow *et al.* 1980: 135-137). From such experiences a practical procedure has evolved. In higher-level systematic studies where only one specimen per species is dissected or examined, one must pay particular attention to variations that are out of line with what is expected (based on the literature or previous experience), especially between species considered closely related. When these occur, additional specimens of the same species should be examined if available, so that the true significance of the variants may be assessed.

III. RESEARCH PROCEDURES

A. Breadth Vs. Depth

In any study there is always the problem of breadth versus narrowness of the data base. One is, for example, not primarily interested in the evolution of the thigh muscles *per se*, but in what they can tell us about the evolutionary history of a group of animals. It is widely believed that concordance among independent data sets indicates a strong hypothesis, so it is always exciting when different workers produce similar phylogenies. One may be tempted, therefore, to study everything in sight, but this can cause problems. An individual is likely to be really authoritative in only one or two fields; a student of muscles may know something about bones, but probably not too much about chromosomes, DNA, or courtship displays. If one tries to analyze too many different things there is a danger of superficiality.

On the other hand, any one system will have intrinsic biases and limitations. Our experience with the limb muscles of birds, for example, shows that there are many parallel developments of derived states, especially reductions and losses, which lead to character conflicts. Comparison with other data can help to resolve these.

How then does one determine the proper balance between breadth and depth, and how does this relate to the use of specimens, for which one has certain responsibilities to the museum that provided them? In my opinion it is better to concentrate on depth, and to give one's major effort to developing a maximal understanding of a single system. Dissection of body parts about which one is poorly informed is a waste of material that could be put to better use by workers for whom they are the specialty. In this way museum specimens will give maximum information, and the needed comparisons can be made between the findings of different workers.

This does not mean that one should not discuss one's data in the context of other findings. The examination of nonconsumable specimens, such as study skins and skeletons, need not be limited by these strictures. However, the consumable nature of spirit specimens dictates that they should not be wasted on casual dissection by workers who are not prepared to use them to maximum advantage.

B. Examination Strategy

Although the following comments refer specifically to muscle dissections, the principles apply equally to any system. What is the best sequence in which to do a series of dissections? When I talk about my research on the limb muscles of birds, someone invariably asks how long it takes me to dissect one limb. I have no answer for this, because I don't first dissect one limb completely, then another, and so on. My approach, rather, is to dissect one muscle at a time through a series of species so that a direct comparison of each muscle can be made among them. Usually a detailed description is written of the muscle in a reference species, and then comparative notes are made on variations in the others. Thus it is unnecessary to write complete descriptions of each muscle in every species. It is important, however, that even the absence of variations be specifically tabulated, and not merely left to the assumption that they occur if not otherwise stated. In this way one will not wonder later whether a condition was unmodified or merely overlooked.

How many species should be dissected at one time? I have found it best to begin with a small number chosen to represent the structural or taxonomic extremes within the group, and to do an initial survey dissection of five or (at most) ten species. This provides a good prediction of the total variation in the group, as well as an indication of the specific structural variations that may be encountered. Such information helps in deciding whether the group has enough variation to make it likely that the study will succeed. If you are studying the phylogeny of a family, start with a survey dissection of one species in each genus; if no significant variation occurs then you have probably chosen the wrong system to analyze. Subsequent dissections would be unlikely to uncover variation within genera if it does not occur among them.

Assuming that sufficient variation occurs to promise the likelihood of success, the next step is to dissect groups of species. Take one subgroup at a time; if too many are compared serially one loses track of variations, even though the reference species is kept in view for comparisons. Most importantly, concentrate first on common forms. Certain kinds of species should not be dissected until the very last. These include forms that are aberrant in structure, such as highly specialized species; forms whose relationships within the group are uncertain; and specimens irreplaceable by reason of extinction, rarity, or geographic inaccessibility. It would be unfortunate to destroy the only available specimen of a form, and later discover the need to recheck some overlooked point. The temptation to dissect the "specials" early is strong, but must be resisted.

C. Anatomical Illustration

Because anatomical work is essentially visual it is important to provide accurate, well-executed illustrations in addition to written descriptions. Even the experienced anatomist cannot follow complex descriptions without visual aids, and the nonspecialist will quickly abandon the effort. Unfortunately photography is not generally adequate for anatomical work. Photographs of bones show the general outlines without problem, but usually cannot reveal details of surface contouring or texture without special techniques. Photography is almost useless for soft anatomy because muscle fiber architecture is generally not apparent, surface reflections of moist tissues obscure structure, there is a lack of contrast between structures, and depth-of-field problems occur. For most anatomical illustration there is no substitute for careful line drawings. Most anatomists are not skillful artists, but adequate line drawing can be learned without excessive trouble, and having to draw pictures of a dissection sharpens the eye to details of structure. Often the dissection of osteological structures can be drawn using a camera lucida attached to the dissecting microscope; this records the shape and proportions of structures accurately. It is probably best to do one's own initial drawings, and then to have a professional illustrator prepare the finished copy for publication. The best choice is a medical illustrator, usually available in the graphics department of a medical school. The importance of first class illustration is such that investigators should routinely request funds to pay for professional work when submitting research grant applications. Nothing detracts more from a study than the publication of amateurish drawings.

How many illustrations are needed, and what should they depict? Drawings of the complete anatomy of the studied region in every species will be impractical in most investigations, but one should not fail to illustrate all of the important structural variations discussed in the text. The practical approach is usually to make a complete set of drawings showing the entire region for one reference species, augmented by drawings of specific characters in other species to exemplify the variations tabulated and discussed. In some cases, however, it may be desirable to do more. Where ambiguity is potentially possible, it is best to make additional drawings. In the case of species that are extinct, rare, endangered, of particular significance in a study, or for which specimens are otherwise unlikely to become available to future workers, it is important to provide thorough and detailed illustrations of anatomical features even beyond that required for minimal character comparisons. Future workers, investigating other aspects, may have only your drawings as a source of information.

IV. PUBLICATION OF RESULTS

Anatomical studies tend to be quite long because of their extensive descriptive material. The high cost of publishing such work often makes it difficult to find an outlet for even the best studies. The problem

may become acute in the case of a young investigator whose reputation is not established; there is a sort of limbo of unpublished doctoral dissertations from years past. The problem is often that the organization of such studies makes it difficult to break them up into separate journal articles.

Nevertheless, anatomical/systematic studies should ideally be published in full, so that all of the data can be made available to other workers. *In the long run, the data may be more important than the analysis.* Systematic philosophies and methodologies are changing rapidly. Current ideological disputes between cladists, pheneticists, and traditionalists may settle out. New statistical and computerized methods are inevitable. Today's most advanced analyses may become archaic in a few years. Those who have done research in this field for more than a decade will probably admit that their earlier work is now out of date methodologically. We have all had the experience of searching old papers for data while disregarding their outmoded analyses. The same fate doubtless awaits our own papers. If the data are provided in full, however, they will be available to future workers to reanalyze according to then-current approaches. For example, I have reinterpreted data originally presented as phenetic similarities in order to assess their possible significance as synapomorphies in cladistic analyses (Raikow 1978, 1982).

Museums should accept more responsibility for the publication of works based on their collections. Most museums have publication series, but access to them is often restricted to staff members or adjunct scientists; the graduate student or collection user who has no official appointment may be left out in the cold. The problem, of course, is funding. Both museums and individual investigators should seek realistic publication funds from granting agencies. Investigators should consider publication to be an integral part of their research program. If they have no realistic prospects of obtaining support for the publication of monographic studies, then they should plan their research from the start for publication in smaller increments as journal articles. In my studies of the Hawaiian honeycreepers (Drepanididae) I published the data and results separately (Raikow 1976, 1977a,b) though it would have been more convenient for both reader and writer to have it all in one place.

If even this is impractical, however, it is still better to compromise than not to publish at all. One approach is to publish a journal article giving the results and discussion, and summarizing the data without presenting them in detail. One can refer the specialist to an unpublished thesis in a university library (available in photocopy) or to notebooks filed in a museum library. We have done this with a few studies (Maurer and Raikow 1981; Swierczewski and Raikow 1981) although full publication would have been preferred.

V. MUTUAL RESPONSIBILITIES OF MUSEUMS AND USERS

What are the responsibilities of museums to those who use their collections, and of the users to the museums? Tensions and misunderstandings sometimes cloud what should be a friendly and mutually beneficial relationship. Museum curators sometimes behave as if their collections exist only for the use of museum staff, and resent requests for the loan of materials. They should remember that museums are resources for the scientific community, are usually supported heavily by public money, and therefore have responsibilities to the community at large. Curators manage their collections, but they do not own them. On the other hand, investigators should not assume that they can expect any and all material to be provided without explaining their needs, and should understand that museums are not mail-order emporia from which one "orders" specimens like holiday fruitcakes. The basic responsibility of the museum is to build and maintain its collections for the use of scientists both in and out of the institution. Curators must develop realistic and consistent policies governing specimen loans. Many museums give preference first to in-house staff, second to outside associate scientists, and third to outside scientists lacking a museum appointment. This is reasonable so long as no one ties up quantities of specimens for long periods. Beyond this the curator must have some basis for deciding whether requested loans should be made; this will depend on the background and scientific reputation of the investigators, and on past experience with their management of loans. Common sense may prevail; one should not ask that irreplaceable specimens be made available for inexperienced students to dissect.

The responsibilities of the user to the museum are: (1) to make efficient use of each specimen, minimizing destruction in the case of dissection; (2) to return specimens when agreed upon, or to obtain permission for their continued use; (3) never to use specimens in a way not agreed upon, as in dissection of body regions not previously approved; (4) to maintain specimens in good condition and to return them to the museum intact and with labels properly affixed; (5) never to allow unauthorized persons to work on

specimens; and (6) when publishing results to give full credit to the institutions and curators who provided the material, and to send copies of the publications to the museums whose specimens were used in the work.

Some curators have suggested that users have an additional responsibility to contribute specimens to the collection, or to replace those consumed by dissection. There is certainly nothing wrong with this, but I would argue against the imposition of such requirements as conditions for a loan. Replacement in kind is absurd; if one had specimens of a needed group, or could collect them oneself, there would be no need for the loan request in the first place. Replacement with other species is possible, but many systematists are laboratory workers and do not go into the field to collect. For these reasons specimen contributions may be suggested, but should not be required. On the other hand it might not be unreasonable for museums to seek financial support from collection users. Museums could establish a schedule of fees to be requested from investigators, who in turn could request such funds in their grant proposals. The situation is analogous to page charges by journals. Like that situation, however, it would be unfortunate if a lack of funds prevented investigators from pursuing their studies. Many journals request page charges from funded workers, but do not refuse publication to those who cannot pay, and museums could adopt a similar policy. Most funding agencies recognize publication costs as legitimate research expenses; perhaps a similar understanding could be developed with regard to the sometimes destructive use of museum collections.

VI. THE FUTURE OF ANATOMICAL COLLECTIONS

What are the prospects that museum anatomical collections will continue to play an important role in the study of vertebrate phylogeny? I believe that they will be very important because: (1) our understanding of vertebrate phylogeny is still very poor; and (2) anatomy will continue to provide important information for phylogenetic analysis. For various views on this question see Ricklefs (1980), McKittrick (1981), and Olson (1981).

Given that we still have a lot to learn about vertebrate phylogeny, what role will comparative anatomy play in the process? For most of the past century comparative anatomy has been the primary source of information used by systematists analyzing phylogeny, but today biochemical and karyological methods threaten to take centre stage. I do not see this as a problem but rather as an opportunity to improve the rigour of systematic work. Hypotheses corroborated by diverse data sets generally inspire greater confidence than those based on the study of a single system. If we study the same group by means of anatomy, DNA hybridization, and chromosome banding, for example, and obtain concordant results, then we will feel secure in our concepts of genealogical relationships. Morphology has still more to offer, however. Once thoroughly tested phylogenies have been established, then structure can also be analyzed in terms of functional adaptation so that the biological significance of historical divergence may be assessed without the problems of confusing common ancestry with homoplasy.

Accepting the future importance of museum anatomical collections, how should their growth be directed? Both conservational and practical considerations of space and cost preclude the indiscriminate collecting expeditions of the past. Museums should continue to emphasize their taxonomic or geographic specialization because no museum can collect everything on Earth. This will most likely lead to thorough coverage of the relevant taxa or regions because curators will know what gaps exist in collections and what groups or regions to emphasize. Museums should include the collection of anatomical specimens as a side activity of expeditions designed for other purposes, such as ecological or behavioural studies. *It is particularly important that museums emphasize more the collection of series of specimens.* Banks *et al.* (1973) found that North American museums contained over 4 million avian study skins, but only 142,150 skeletons, and a bare 52,025 spirit specimens. This often means that one can obtain only a single specimen of a needed species, in which case the museum may well put severe restrictions on the extent to which it may be dissected, or may even refuse to let it leave the building. For forms that are not endangered or threatened, series are desirable for several reasons. First, it is sometimes important to examine variation within a species. Second, unusual features are occasionally found which could represent either individual anomalies or normal peculiarities of a species. Third, sometimes a specimen is damaged, so that others are needed to fill gaps in information. Finally, it is desirable that anatomical information be verifiable by other workers.

Museum collections of vertebrate anatomical material are far from adequate in view of the work that remains to be done. For example spirit and skeleton collections each lack specimens of about one-fourth the living species of birds, and for many more there are no series. It should be clear that the need for building up collections continues, and should be pursued vigorously. It is collection-based research that sets museums apart from other types of institutions, and only careful planning for the continued growth of these collections will insure their future usefulness to students of vertebrate morphology and systematics.

VII. SUMMARY

Practical suggestions are offered for the use and curation of museum anatomical collections. The search for specimens is cumbersome at present, but computerized inventories are beginning to make it easier. The choice of specimens depends on relevance and availability and, in the case of dissection specimens, ease of replacement. Because spirit specimens are destroyed by dissection, particular care must be used in their study, and cooperation between workers can maximize their usefulness. Older specimens in many museums were poorly fixed, and collectors have sometimes preserved only those specimens not suitable for preparation as study skins. The time required for dissection makes the analysis of large series of spirit specimens impractical, and the investigator must be sensitive to the possible meanings of unexpected anatomical variations. It is better to do a thorough analysis of one body system than a superficial study of several. Comprehensive dissections of numerous species should be preceded by survey dissections of a few representative forms. Illustrations are a crucial but time-consuming part of anatomical studies. The length of many morphological/systematic studies may cause problems in their publication, but data should be published in full detail because in the long run their usefulness may outlive that of the conclusions drawn from them. Museums and investigators should be more aggressive in seeking funds to support publication. The basic responsibility of a museum is to build and maintain a collection useful to workers both in the institution and outside of it. The basic responsibility of collection users is to respect the agreements under which specimens are provided. It may be desirable to establish a system of user fees to help museums support their collections. The recent development of non-anatomical systematic methods will not diminish the importance of anatomical studies, but will provide new data to test and complement the findings of morphologists. Museum anatomical collections are not adequate for their potential future use, and continued collecting is required.

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10. ADAPTIVE INFERENCE AND MUSEOLOGICAL RESEARCH

W.J. BOCK

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I. INTRODUCTION

A history of the earliest curio cabinets and natural history museums reveals that adaptations of living and fossil organisms were of major interest to the first museum biologists. This interest remains unabated to the present although much of the research on individual adaptations is done now by non-museum biologists. In addition to possessing representative taxonomic specimens of animal and plant species, collectors were especially anxious to have the unusual, the peculiar, and the bizarre, both as taxonomic and as anatomical specimens. As they mused over museum specimens of these strange organisms, biologists were led quite naturally to questions of the functions of peculiar features and of their advantages to the species possessing them — what benefit could such structures confer to the organism? Such considerations directed museum naturalists back to observations of "normal" structures whose functions, biological roles, and adaptive meaning were more readily understood. The greatest success in the effort to comprehend functions and adaptiveness was reached for obvious features such as wings in birds and bats, fins in fish, ichthyosaurs, and whales, the long neck in giraffes, etc. Reasonable functional and adaptive explanations have been provided for a number of peculiar features such as the elongated knife-like mandible of the Black Skimmer (*Rynchops nigra*) (Zusi 1962), the ventrally angled "Roman-nosed" bill of flamingos (Phoenicopteriformes) (Jenkin 1957), the abrupt bend to right of the bill of the New Zealand Wrybill plover (*Anarhynchus frontalis*) (Pierce 1979), the asymmetrical cross-bill and jaw muscles of the Hawaiian honeycreeper (*Loxops coccinea*) (Richards and Bock 1973), electric organs of fish (Møller 1980), sun-bathing behaviour of Old World vultures (e.g. *Gyps bengalensis*) (Houston 1980), the broadened incisors of the chisel-toothed Great Basin Kangaroo Rat (*Dipodomys microps*) (Kenagy 1972, 1973), and the elongated ribs supporting the lateral trunk airfoils of the living *Draco* and the fossil *Icarosaurus* (Colbert 1967, 1970). But functional and adaptive explanations have remained far more elusive for numerous features such as the long tusk of the Narwhal (*Monodon monoceros*) (Best 1981), the heavy ivory-like casque of the Helmeted Hornbill (*Rhinoplax vigil*) of Malaya and the East Indies (Manger Cats-Kuenen 1961), the elongated incisors of saber-toothed cats (*Hoplophoneus*, *Smilodon*, *Machairodus* among others, Felidae) (Romer 1966), the very thick skull roof of dome-headed dinosaurs (*Pachycephalosaurus*), the cranial crest of duck-billed dinosaurs (hadrosaurs) (Ostrom 1961, 1962, 1964), the nuchal shield of horned dinosaurs (ceratopsians) (Colbert 1948; Ostrom 1966) and, perhaps the strangest of all structures, the elongated dorsal spines of the trunk vertebrae and associated sails of *Dimetrodon* and other pelycosaurs (Pelycosauria, Synapsida), of *Ouranosaurus* (Ornithischia) and of *Spinosaurus* (a carnosaur, Theropoda), a feature which evolved in three different groups of reptiles at three different times (Swinton 1970; Halstead 1975; Charig 1979; Halstead and Halstead 1981). These lists could go on and on, limited only by how well one can recall the literature, and by the patience of the reader.

The existence of this great diversity of features from the normal to the bizarre, many of which could be shown to be adaptations — i.e. features important or essential to the survival of the organism as an individual — was a major impetus for nineteenth century biologists thinking about the possibility and the mechanisms of evolutionary change. The fact that these adaptations may vary in their degree of perfect-

tion, may be different according to the environment, geography, and presumed affinities of the organisms, or at times may be present or absent for no apparent reason, led to a series of interrelated questions about the nature of adapted features and about the possible mechanisms underlying their origin, their subsequent perfection, and their occasional loss. These questions were among the major ones for which Darwin and other early evolutionists were seeking answers.

As evolutionary theory became better established, museum workers and other evolutionary biologists delved more deeply into details about the nature of adaptation and of adaptive evolutionary change, the role of preadaptations, the structure of adaptive radiations, the nature of thresholds in adaptive shifts, the concept of key adaptive innovations, *etc.* These ideas became increasingly central to studies in comparative biology and systematics, especially in classification of the higher categories (above the generic level). Although the dominance of museum biologists in this research has declined in recent decades, museum specimens (often anatomical ones) of recent and fossil species have remained central to the study of adaptation in its broadest sense, and to the discovery of individual adaptive features. These specimens are essential for the formulation of hypotheses about particular adaptations or about adaptive changes, because a knowledge of the feature is needed before any attempt can be made to postulate its possible adaptive nature. The study of museum specimens and all work that can be done in museum laboratories, *e.g.* functional analyses, provide an important part of the empirical evidence needed to test hypotheses about adaptations and adaptive evolutionary change.

In this paper, I will summarize the ideas associated with the concept of adaptation and will discuss the roles of museum specimens and of museum research for the study of adaptation. Attention will be given to special preparation and other requirements in obtaining, treating, and studying anatomical specimens, what conclusions can and cannot be reached on the basis of museum work alone, and the relationships between adaptive inferences to other museum-based research. Unless otherwise specified, the term museum specimen in this paper will imply only those that have been specially prepared for anatomical study, *e.g.* cleaned and dried skeletons, formalin-preserved bodies, *etc.* Although my discussion will be restricted to specimens of vertebrates, the conclusions should be valid for all groups of plants and animals.

II. ADAPTATION AND ASSOCIATED CONCEPTS

Before it is possible to discuss the roles of museum specimens and museum work in adaptive inference, the concepts of adaptation and adaptive evolutionary change, and a series of associated ideas must be set down. Much of the following discussion is based on my earlier papers (Bock, 1959, 1965, 1967, 1969, 1970, 1972, 1976, 1977a, 1977b, 1979, 1980a, 1980b, 1981; Bock and von Wahlert 1965), to which the reader is referred for additional details. Formulation of useful concepts in science depends on making them sufficiently general so that they can apply to a large class of objects, but not so general that they lose all explanatory meaning. Hard and fast formulae for attaining these goals do not exist. A major problem in the development of ideas associated with biological adaptation has been in achieving this balance.

Historically, even well before the idea of organic evolution was accepted by biologists, adaptation was used to describe phenotypic features of an organism which contributed to the survival of that organism as an individual. As evolutionary theory developed, biologists realized that adapted features contribute to the fitness of the individual organism (but adaptation is not the same as fitness), that adaptation and fitness apply to different levels of biological organization, and that adapted features are not the only class of features which contribute to fitness. The concept of fitness applies, of course, to the number of offspring (= copies of one's genes) that an individual contributes, either directly or indirectly, to the next generation. Adaptation does not apply to the genotype, to individuals, to populations, to species, or to groups of species (communities). The adjective adaptive has been applied to many terms in evolutionary discussions, such as "adaptive genes," and relative expressions such as "the individual (or the species) is adapted," are used, but these statements do not have a precise meaning within evolutionary theory, nor do they connect in any definite way to other evolutionary concepts.

If adaptiveness and adaptive evolutionary change are properties descriptive only of phenotypic features of individual organisms, then it is necessary to dissect apart the attributes of these features and their relationship to the agent to which these features are adapted. Let me be clear at the onset that the

concept of adaptation makes sense only if adapted features are judged relative to selective agents arising from the external environment of the organism. If the concept is expanded so that one feature can be adapted to another feature of the same organism, or that features can be adapted to the "internal environment" of the organism (which is actually another feature), then the notion of adaptation becomes so broad that its meaning becomes vague and its usefulness within evolutionary biology all but disappears.

An adaptation (the state of being) is a phenotypic feature of the individual organism. By feature, I mean any trait of the organism properly described, not only a morphological structure. It is possible to speak of physiological traits or of behavioural traits as adaptations because they are phenotypic features of the organism. In all cases, the properties of form and function of the trait must be described carefully. In the case of behavioural traits, usually only the observed behaviour is described but this must be recognized as a shorthand description. A proper description of a behavioural trait should include all connections in the central and peripheral nervous systems and the skeletomuscular and other morphological structures required to carry out the behaviour.

The first step in any adaptational analysis is to delimit properly the feature whose possible adaptive significance is being considered. No rules exist on how to recognize individual adaptive traits; these are usually not concordant with individual morphological features, but with functional complexes of morphological features. This problem of sorting out unit adaptations is akin to the recognition of unit taxonomic characters, a matter well known and of great concern to systematists. It is not valid to assume that adaptive conclusions can be reached about any phenotypic trait chosen arbitrarily and studied in isolation of all other features of the organism. Not every feature is an adaptation and not every describable attribute of a feature interacts with a selective agent of the external environment. Individual phenotypic traits may be present for many different reasons including developmental and structural requirements. Numerous attributes of features, such as the red colour of hemoglobin, the sound of the beating heart, and the electrical field generated by contracting muscles, do not, in most organisms, have a biological role that establishes the necessary feedback relationship with an environmental factor and does not form a synerg with the resulting selective agent. Hence such attributes cannot have any adaptive significance. That each and every phenotypic trait of an organism must be an adaptation (*i.e.* explained adaptively) was never a proper claim of the "adaptationist programme" contrary to the assertions of Gould and Lewontin (1979).

In some cases, it is possible to analyze the adaptive significance of single morphological features studied in isolation of other features, as for example, the adaptiveness of the salivary glands for food storage during winter in the Gray Jay (*Perisoreus canadensis*) (Bock 1961; Dow 1965), or the adaptiveness of the sublingual pouch for food carrying to storage areas in Clark's Nutcracker (*Nucifraga columbiana*) (Bock *et al.* 1973). In other cases, perhaps the sizable majority, individual traits must be analyzed within a larger functional complex of features before their adaptive significance can be understood properly. For example, the adaptive meaning of the ectethmoid articulation of the mandible in *Melithreptus* (Meliphagidae) (Bock and Morioka 1971) was obscure until we included the salivary glands, the jaw apparatus, and the tongue apparatus in our analysis. The traditional division of morphological features into skeletal elements, muscles, ligaments, nerves, *etc.* is for convenience of description and instruction only, and is usually not suitable for adaptive analysis. In most cases, these features must be reassembled into proper functional complexes before valid adaptive inferences can be reached — that is, a suitable holistic approach is needed (see Dullemeijer 1974, 1980; Gutmann 1977, 1981; Gutmann and Bonik 1981; and Homberger (1985) for additional comments on holistic approaches in functional adaptive morphology). However, it is not valid to push the holistic approach to its extreme and to claim that adaptive explanations of individual traits are not possible unless one studies the whole organism as advocated by Gould and Lewontin (1979). A functional-adaptive analysis of the nose of the Black Rat (*Rattus rattus*) can be done very well without consideration of its toes (see Bock and Homberger 1985; Mayr 1983).

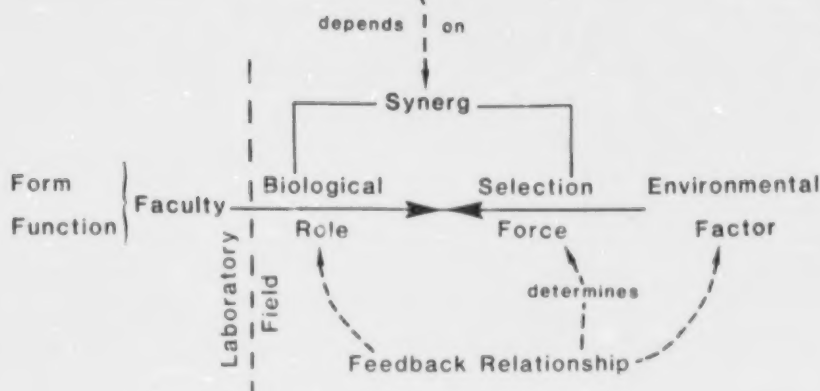
The adaptation is a phenotypic feature of the organism and as such is a form-function complex (see Figure 1). It is not proper to speak of morphological adaptations, physiological adaptations, or behavioural adaptations because such terms imply that partial properties of features are adaptations whereas only the complete feature, considering all of its properties as a single unit, can be the adaptation. Not only must a feature, such as a skeletal element, be properly integrated with other features such as muscles, articulations, ligaments, nerves, *etc.* into proper functional units when analyzing its adaptive significance, but the feature must also be subdivided into its component subunits and the adaptive nature of each part must be considered. A bone, such as the giraffe's femur for example, must be decomposed into its outer shape and size, sites for muscle and ligament attachment, articular condyles, internal ar-

ORGANISM

ENVIRONMENT

Feature = the adaptation

Umwelt



Organism = Sum of the synergs = Niche

Laboratory studies

Descriptive and functional morphology to determine:

- a) the form(s) = the spectrum of all possible forms during life
- b) the function(s)
- = solving the "black box" of the organism at all levels of organization

Field studies

Behavior and ecology to determine:

- a) the biological role(s)
- b) the environmental factor(s) acting on the organism
- c) the feedback relationship(s) and the selection force(s)
- d) the synerg(s) - the interactions between the biological roles and the selection forces

Both are required to determine the adaptation

Fig. 1. Simplified scheme to illustrate the components of an adaptation (state of being), and the range of museum laboratory and field studies required for the synthetic determination of an adaptation. The adaptation is a feature of the individual organism and depends on the properties of the synerg, i.e. the adaptation is relative to a selection force arising from the environment. The selection force is a demand placed on the organism by an environment factor with the exact properties of the selection force determined by the nature of the feedback relationship established between the organism and the environmental factor via the biological role. After the adaptation has been established, additional study is needed to ascertain (measure) its degree of goodness. (From Bock 1977a, 1980a.)

range of trabeculae, etc., and the adaptiveness of each part considered. If a feature such as the brain of *Homo sapiens* can be shown to be adaptive with respect to particular selective agents, it does not necessarily follow automatically that all parts of this feature are adaptive to these or any other selective agents.

The first step in the analysis of any suspected adaptation is to describe carefully and fully the properties of form and function of the feature (or functional complex of features) as summarized in Figure 1 (see Bock and von Wahlert 1965; Bock 1977b, 1979, 1980a; the reader is referred to these papers for formal definitions and further discussion of the concepts of the form-function complex). Museum specimens are essential for this part of adaptational analysis especially when any comparative foundation is needed, as in studies of adaptive change.

The description of morphological form, especially for adaptive inferences and associated studies, is far more complex than realized by many museum biologists. It is not simply just a matter of looking at the feature and describing what is seen. Rather, one must know which attributes of the feature are and are not relevant to the particular type of study. For adaptive inference and related analyses, description of morphological form must be done in light of knowledge of the general functional properties of that class of structures, e.g. the physiological attributes of striated skeletal muscles. Unfortunately much of the morphological description presented by museum and other workers studying suspected adaptations fails this critical requirement, and is largely sterile for any adaptive analysis or additional work dependent on these inferences. One can read description after description of the morphology of the vertebrate skeletomuscular system without finding the information needed for even the most elementary functional analysis, and hence for drawing any adaptive inferences. The consequence of this failing for adaptive research cannot be overemphasized. Until this shortcoming in description of morphological form is resolved, progress in adaptive inferences will be greatly restricted.

A related problem is the establishment of detailed correlations between the variables of form and of function. These can be determined only with suitable comparative morphological description and physiological investigation. I will discuss this point later.

A largely ignored problem is the range of morphological form possible within a single individual, a question quite separate from that of individual variation which is well understood by museum workers. The problem of the range of morphological form arises because most descriptions are made strictly from preserved specimens, and because few anatomical specimens of a species are usually available for study; hence the common belief that features have a single fixed morphological form in an individual organism. Setting aside artifacts resulting from captivity or preservation, almost all features have a broad spectrum of possible morphological form in a single individual living in its normal environment although this spectrum of form is not present at any one time (Bock and von Wahlert 1965). This range of morphological form results from developmental changes, wear, physiological (= somatic) adaptation arising from environmental modification, normal physiological activity such as muscle contractions, filling and emptying of the digestive tract and other internal organs, external environmental forces such as air and water pressures, and many other factors. In addition to the range of form of individual features, alterations of location and other relationships between individual features such as the position of bones, angle of attachment of muscles, etc., must be included in the spectrum of form in any description. The total spectrum of morphological form must be included in any description because both the functional properties and the adaptive significances of the feature change with alterations in its form during an individual's life.

The concept of function continues to be a major hassle in adaptive analysis. Function is used to denote at least two quite distinct concepts, that of the operation or action of the feature [= functional properties as I restrict it (Bock and von Wahlert 1965: 273-276; Bock 1980a: 219)] and that of the feature's use by the organism in its normal environment [= biological role (see Bock and von Wahlert 1965: 278-279; Bock 1980a: 219)]. It is simply not possible to develop consistent ideas about adaptation and adaptive evolutionary change with these overlapping and conflicting notions of function. Some workers (e.g. Dullemeijer 1974, 1980) continue to advocate a vague definition of function which makes its use ambiguous and hinders development of adaptational theory. I advocate a strict restriction of the concept of function to the set of chemical and physical properties of a feature arising from its properties of form. This definition is very close to the concept of function in standard use by physiologists, and permits the formulation of a consistent and usable set of concepts needed for the development of adaptational theory. No other definition of function has proven to be more fruitful for this purpose.

Determination of functional properties can be achieved in several ways. The best is by direct observation using a series of techniques, including cinematography, electromyography (EMG), recording of

forces and pressures, and many other (usually biophysical) methods being developed in the rapidly expanding field of functional morphology. This work lies largely outside of usual museum research but must become standard if progress is to be made in adaptive inference.

The second major method to determine functional properties is by inference from the morphological form using established correlations between the properties of form and of function made by direct observations. Functions established by the inferential method do not have the same degree of certainty as those determined by direct observations. However, this method is the only one possible for fossil species and for the bulk of living species which cannot be studied directly because they do not survive under laboratory conditions, are too rare or endangered to permit use of the large number of individuals needed for many functional observations, etc. The importance of this method underlines the necessity of careful morphological description of species for which direct functional observations are possible, so that the essential form-function correlations can be established. Successful application of the inferential method in species for which functional properties cannot be observed directly depends on careful, complete description of morphological form, with a knowledge of those attributes of structural form needed to permit successful functional inferences. Much of the work in functional morphology, especially comparative analyses, which can be undertaken with museum specimens depends on the inferential method. Museum workers who lack the facilities and equipment to make direct functional observations, or are studying species for which such observations are not possible, must master the details of the inferential method if they desire to undertake adaptational studies.

The following concepts lie outside work that can be done with museum specimens, but are no less important to the study of adaptation. In many cases, these aspects of field biology are best done by ecologists in collaboration with museum biologists (Bock 1977a).

Combinations of the forms and functions of a feature comprise its faculties. The use of these faculties by the organism in its normal environment constitute the biological roles of the feature. These biological roles interact with environmental factors of the *umwelt* of the organism in a complex feedback relationship which depends on the nature of the environmental demands on the organism and on the characteristics of the biological role. This feedback relationship determines the exact details of the selective agent that arises from the environmental factor and interacts with the biological role forming a link that may be called the *synerg*. It is important to realize that the details of the selective agent are not determined unilaterally by the environmental factor, but by the feedback relationship between it and the biological role (von Wahlert 1965). Depending on how different organisms react to it with their biological roles, the same environmental factor can give rise to radically different selective agents. And finally the existence and degree of perfection of an adaptation — the phenotypic feature — depend on the synerg. A feature is an adaptation with respect to a particular selective agent that has formed a synerg with a biological role of that feature. The essential aspect of an adaptation is that it permits the organism to maintain a successful synerg between a biological role of that adaptation (feature) and a stated selective agent. Successful means that the individual organism continues to survive as an individual. Success is relative and some measure of success or degree of precision (goodness) of the adaptation is needed. Clearly adaptations are not an absolute all-or-nothing relationship and it is foolish to postulate that adaptations always are (if ever) maximal, best or optimal. Measures of the degree of goodness of adaptations must be independent of other evolutionary measures, notably that of fitness. Several measures have been suggested, for example the amount of energy needed to maintain the synerg (Bock and von Wahlert 1965), the ratio between energy gained versus energy expended especially for feeding adaptations (Bock 1979, 1980a), or by a direct competitive test between individuals differing in their adaptations.

According to the tenets of evolutionary theory a direct relationship exists between adaptation and fitness, in that individual organisms possessing the better adaptations will on the average have greater fitness. Nevertheless adaptations (= survival features) are not the only features that are linked positively with fitness. At least two other classes of features exist which correlate with fitness; these are reproductive features and kin features (Bock, in prep.).

The same adaptation need not evolve in response to the same selective agent acting on different groups, rather morphologically different ones may evolve depending on genetically and other chance-based differences in the several groups. These different adaptations to the same selective agent represent multiple pathways of evolution (Bock 1959), and have been called *paradaptations* (Bock 1967). Not all differences observed among features of different species are adaptive, many are *paradaptive* differences resulting from accidental evolutionary causal mechanisms such as mutation, recombination, and other genetical events [see Mayr (1962) for a discussion of chance versus design in evolution].

Adaptive evolutionary change is more difficult to characterize as this term has been used for a wide range of evolutionary phenomena. In general, it means any evolutionary change under the control of a selective agent. In a restricted sense as applied to individual features, it means any modification in the form-function complex of a feature (adaptation) which improves the degree of goodness of that adaptation depending on how it is measured, e.g. amount of energy needed to maintain the synerg. This change must be under the control of the selective agent to which the feature is adapted.

Many workers (e.g. Munson 1971; Gould and Vrba 1982) insist that for a feature to be an adaptation (state of being) it must have evolved adaptively with respect to the same selective agent. This assumption is based on a confusion between the concept of adaptation as a state of being, which is a nomological-deductive scientific explanation, and the evolutionary history of that adapted feature (whether it evolved adaptively or by some non-adaptive process) which is a historical-narrative scientific explanation (Bock 1980a: 224). Clearly the notion of an adaptation and the recognition of individual adaptations are independent of how these adaptations come into being just as any nomological-deductive explanations about molecules of water are independent of the origin of these molecules, be it by the oxidation of hydrogen or by the decomposition of hydrogen peroxide. Understanding that the state of being adapted and the process of becoming adapted are not necessarily coupled is most important for postulating processes of change and for developing narratives of particular historical events. The whole approach to adaptive inference is simply not possible without a firm appreciation of the independence of adaptation as a state of being and as a process (Bock 1980a, b).

This independence is clearly seen in the concept of preadaptation (Bock 1959, 1979), which connotes features that have acquired a suitable form-function complex which permits establishment of a synerg with a particular selective agent whenever it appears. Features reach a preadapted condition fortuitously and under the control of selective agents other than the one to which they are preadapted. Preadaptation has a major role in evolutionary theory because most (all ?) adapted features pass through one or more preadapted stages in their evolution. The term exaptation (Gould and Vrba 1982) appears to be a junior synonym of the well established term preadaptation.

A few additional terms must be mentioned although these are less critical for adaptive inference. Adaptive radiation refers to the evolution of a diversity of morphologically different species in a monophyletic group. The assumptions are usually made that morphological forms are adaptive and that they arose by adaptive evolution, but these are rarely supported with any real evidence. Moreover, no guidelines have been established as to what constitutes an adaptive radiation and how one is recognized.

Closely associated with the idea of adaptive radiation is that of the key innovation. This is a feature, usually assumed to be adaptive, whose existence is essential to the subsequent adaptive radiation. Clearly there are features, such as feathers in birds and the set of extraembryonic membranes of the amniotes, which have great evolutionary potential and appear to be critical to subsequent radiations. But the exact role of the key innovation in all of the descendant adaptations is usually not clarified. Nor does a reasonable set of rules exist by which key innovations can be recognized and distinguished from other adaptations. Closely related to, and perhaps identical with, key innovations is the concept of general adaptations — these are in contrast to special adaptations (Brown 1958). General adaptations evolve at the origin of a group and in some way are fundamental to its radiation, while special adaptations are characteristic of individual members of the group. The definitions of general and special adaptations are usually somewhat vague, but most importantly a reasonable set of rules by which such features can be recognized does not exist.

III. RECOGNITION OF ADAPTATION

A series of theoretical concepts about biological adaptation, no matter how carefully developed, is of little use in the absence of a set of methods by which individual adaptations can be recognized and by which particular adaptive evolutionary changes postulated.

Several general methods are used by biologists to identify individual adaptations; these are the comparative, the correlative, and the synthetic (see Bock 1977a,b, 1980a). Of these methods, the only valid one is the synthetic approach. The synthetic method requires an in-depth study of the properties of form and function of the feature (see Figure 1), its biological roles, the environmental factors that act on the organism, their feedback relationships with the biological roles, the resulting selective agents, and the synergs formed between the selective agents and the biological roles. After the adaptation has been

established, its degree of goodness must be determined using some suitable measure. Although the rules of the synthetic method by which adaptations can be recognized are relatively simple, the actual analysis of suspected adaptations can be most difficult, and usually is. Aside from obvious, trivial ones, relatively few adaptations have been established with sufficient rigor. It is not a valid research strategy to abandon search for the adaptive nature of a particular feature after a few attempts, and to conclude that this feature does not have an adaptive meaning, as advocated by Gould and Lewontin (1979). Rather one can postulate a nonadaptive conclusion only after a very thorough and exhaustive attempt to establish the adaptiveness of the feature. The recent, most interesting demonstration that the adaptive significance of sun-bathing behaviour of griffon vultures (*Gyps*) is associated with straightening deformed flight feathers (Houston 1980), illustrates the need for exhaustive studies before abandoning the search for an adaptive explanation. In this case, Houston had a brilliant insight into the function and the adaptiveness of sun bathing in these vultures. Most biologists would have struggled with this feature for years before discovering its adaptive significance, and many might never have discovered it.

Demonstrating that a feature is an adaptation to a particular selective agent requires detailed study in the laboratory to describe its form and functions, and in the field to discover its biological roles, the environmental factors acting on the organism, the selective agents, synergies, etc. The most efficient system of study appears to be teams of researchers, who divide the project into its laboratory and field portions (Bock 1977a). Most workers do not have the training to undertake all phases of research needed to demonstrate an adaptation. A survey of numerous studies propounding adaptations reveals that most of these studies lack important components of the needed analysis — if the description of the form and functions is well done, the field analysis is weak or lacking, and vice versa. Consequently even if the conclusion about the adaptation is correct, it has often not been supported sufficiently.

As difficult as demonstrating individual adaptations may be, the establishment of an adaptive evolutionary change of a feature is far more difficult. First a reasonably valid phylogeny of the features must be postulated; in many cases this must be a presumed or pseudophylogeny based on a comparison of living organisms. Second is to demonstrate the adaptive nature of the features at each stage in the phylogeny, including an assessment of the degree of goodness of the adaptation at each step. It is essential to state the exact selective agents to which the feature is an adaptation at each stage in the phylogeny. Lastly, one must show that the evolutionary change from one step to the next in this phylogeny of adaptations has been under the control of the selective agents associated with the adaptation at each successive stage. It is quite possible to demonstrate that a feature is adapted to the selective agents acting at each of two successive stages in the phylogeny, and yet the evolutionary change from the earlier to the later period is not under the control of the selective agents acting at this latter time. Hence the change is not an adaptive one (= process) with respect to the selective agent to which the feature is now adapted (= state of being). Instead the observed evolutionary change is a pleiotrophic consequence (by-product) of other presumably adaptive evolutionary modifications. The evolution of a feature to a preadapted condition with respect to some particular selective agent, represents a nonadaptive change which is the by-product of other presumably adaptive evolutionary change. To conclude that the evolution of a feature from an ancestral to a descendant morphological form is adaptive, it is necessary to demonstrate that this evolution was under the control of selective agents to which the descendant feature is now adapted. This type of adaptive inference is very difficult indeed, and it is hard to find and cite strongly conclusive examples aside from those representing continued specialization of the same adaptation. Many examples of adaptive evolutionary changes in the literature are probably valid, but the supporting evidence and arguments are not sufficiently rigorous.

IV. THE ROLE OF MUSEUM SPECIMENS

Conclusions on adaptations based strictly on study of museum specimens of living and fossil organisms are still being offered. Clearly such conclusions are not valid and need not be discussed further. Of greatest importance are the questions: What part does study of museum specimens have in the broad spectrum of research needed to formulate and test adaptive inferences — both of the state of being and the process? And how essential is this role? Study of museum specimens, no matter how thorough, can provide only the information associated with the laboratory side of the research program (Figure 1). And in most studies, only a description of the morphological form — and frequently an inadequate description

— results from study of museum specimens. These materials do not permit direct observations of functional properties, and few museum biologists have the facilities or the abilities to undertake direct observation of function in their analysis of suspected adaptations. A critical turning point for future development in museum research exists here. Currently an important revival is taking place in anatomical research using museum specimens. Museum biologists are realizing more and more the importance of anatomical specimens, are enlarging these collections, and are encouraging research. Yet, most of these studies are pure description of morphological form which do not even consider those attributes needed for functional analysis. Unless a strong effort is made to expand the facilities and equipment needed for direct observation of functional properties and to train museum biologists doing anatomical research in the background and techniques of functional analysis, the current revival in museum morphological studies will be still-born.

One approach of functional analysis that must be developed for work on museum specimens, and one that can be done quickly and with relatively little expense, is the inferential method. This method is needed because it is not possible to make direct functional observations on many species (e.g. rare and endangered species) of interest to museum biologists in their work on adaptive inference. At this time, it can serve as a means to stimulate interest in functional investigations and to permit research in this area during the period required to equip museum laboratories with the facilities needed to do direct functional observations. Work must be started by morphologists to improve the form-function correlations needed for the inferential method of functional analysis. And museum biologists interested in adaptational research must begin to use the inferential method at once to deduce functional properties from the analysis of morphological form.

Although study of museum specimens alone is not sufficient to develop and test conclusions about individual adaptations, it is an essential part of this work. Adaptations cannot be recognized in the absence of knowledge of the forms and functions of the features. Moreover study of museum specimens is the most efficient means of discovering new features which may prove to be adaptations, examining the diversity among adaptations, establishing the sequences of change needed to study adaptive evolutionary modifications, *etc.* Basically, study of museum specimens is the most important way, by far, of postulating hypotheses of all types about adaptations. It is doubtful that any other area of research will ever surpass study of museum specimens as the primary source of adaptive inferences. Comparative analysis of museum specimens is the only way to establish the phylogenetic and adaptational patterns of adaptive radiations.

V. SPECIAL REQUIREMENTS OF ANATOMICAL SPECIMENS AND OF MUSEUM MORPHOLOGICAL RESEARCH

Collections of anatomical specimens began as special collections in institutes or departments of human anatomy attached to universities, as collections in departments of comparative vertebrate anatomy in natural history museums, and as reference collections (mainly skeletal collections) in departments of paleontology in natural history museums. With a change in tradition, departments of comparative vertebrate anatomy disappeared in natural history museums, and their collections were divided among the several taxon-oriented departments. And many of the collections in departments of human anatomy and of zoology were transferred to natural history museums and subdivided. Paleontology departments relied more and more on the anatomical collections of departments of living organisms for the comparative collections needed to identify fossils, although many still maintain a reference collection of skeletons.

As a result of the changing tradition, special anatomical collections developed slowly alongside the general collections of taxonomic specimens. The anatomical collections were increased erratically with many specimens consigned to them only when they were too damaged to make good skins. A bias existed for anatomical specimens of species whose taxonomic status was uncertain, with the result that collections are often top heavy with specimens of peculiar species, but lack a representative sample of the normal diversity in a group. Many museums built up large collections of cleaned and dried skeletons while ignoring whole spirit specimens. And because of space restrictions, few spirit specimens of large animals are obtained. It is not only a question of storing spirit specimens of whales and elephants, but a matter of preserving and storing specimens larger in size than 10-20 kilograms.

Many of these problems have been ameliorated over the past 25 years with special efforts being made to collect anatomical specimens, and to build up and properly curate the anatomical collections. Collections are becoming more representative, undamaged specimens are being chosen for anatomical specimens, spirit collections are being increased, and greater care is being given to the preparation of specimens. Some problems still exist including obtaining specimens of rare and endangered species, and obtaining and storing spirit specimens of large animals. Some special problems exist for museum specimens if they are to be used as the basis of adaptive inference.

Most essential is that the specimens be normal, individuals from the wild, which have been subjected to the usual set of environmental factors acting on the species. Specimens of zoo animals, cripples, diseased individuals, oil-covered birds, carcasses found along beaches, *etc.*, should not be used for adaptational studies because of possible modifications in the features [*i.e.* physiological adaptations (Bock and von Wahlert 1965)] during the period of the animal's life in which they were subjected to these abnormal conditions. Moreover, it is likely that such specimens represent a nonrandom sample of the species such as the storm-killed House Sparrows (*Passer domesticus*) reported by Bumpus (1899). It is especially important to note that zoo individuals live in a regime very different from the environmental conditions characteristic for the species, and are fed a diet that is usually strikingly dissimilar from that of wild individuals in terms of food items, amounts, and regularity. All of these factors can have effects on the structure of the body, so that the observed morphology can differ considerably from normal.

Environmental conditions of normal free-living individuals vary greatly and this can have large effects on their morphology. Summer and winter individuals, breeding and nonbreeding ones, those living under optimal conditions compared to those under harsh conditions, *etc.*, will be subjected to considerable variation in environmental demands, which will influence their morphology. Just a simple morphological variation as the amount of body fat and hence weight of birds can be doubled in an individual in prime condition to start a migratory flight, compared to one that has just ended a long and strenuous one. A similar difference is observed in mammals before and after winter hibernation. All of these variants are natural and lie within the range of adaptation of features of the species; hence it may be necessary to sample the whole spectrum of morphological form when analyzing the adaptiveness of the feature.

A second problem associated with preservation of museum specimens is that the specimens should be preserved in a comparable way. If possible, standard preserving fluids and procedures should be used, and standard storage fluids should be used for spirit specimens. However, such standardization may not be possible, but the resulting variation may be too small to be of any real concern. Of far greater importance is that specimens be arranged in the same standard position before preservation. This will insure a comparable arrangement and orientation of muscles and other structures whose morphological form changes considerably during normal physiological operation. The shape of jaw muscles depends on whether the jaws are closed or fully opened when the specimen was preserved. The same is true for tongue muscles, depending on whether the tongue is in the normal position within the mouth or fully extended. Limb muscles vary depending on whether the limbs are fully flexed or extended. These differences affect not only the gross appearance of the muscles, but also such important measures as fiber length, fiber cross sectional area, angle of pinnation, and others at the level of fine structure. This lesson was made clear to me when I dissected a second specimen of *Toxorhamphus novaeguineae* (Meliphagidae), an Australian honey-eater with a very long tongue and elongated tongue muscles. The tongue muscles of this specimen were drastically different from those in the first specimen I dissected. Only when I realized that the tongue of the second specimen was fully extended out of the mouth when the bird was preserved did I understand the basis of the observed difference. The problem of standard preservation position is relatively easy to solve, but requires agreement on how the specimen should be arranged prior to preservation. But it is essential that once a standard is established for a group, it is followed closely.

Systematists have realized for decades that large series of taxonomic specimens are needed to establish the amount of individual variation. The same is true for anatomical specimens. Such series are being assembled for dried skeletons, but much more slowly for spirit specimens. These series are needed not only to establish the degree of individual variation among individuals, but the range of modification of the feature within a single individual. Some of this work has been done for individual variation in skeletal structures, but very little for the soft anatomy, including muscles, and almost nothing for the range of modification within the individual.

Several special problems exist in studies of museum specimens for work on adaptive inference. Some of these hold for all morphological study of museum specimens no matter what the purpose may be. A general problem is that in all too many cases, only a single spirit specimen is available for dissection. In

these cases, it is necessary to dissect the structures in a series of specimens of some common, closely related species to learn the details of the morphology and its variation. Moreover, some ideas for the form-function relationships should be obtained from study of the common species. These preliminary studies will provide a base for dissection and description of the unique specimen to insure that a maximum amount of information is obtained and that no significant structural attributes are missed during dissection.

Anatomical dissection and descriptions for adaptive inference must be done with a knowledge of the pertinent form-function correlations. Moreover it is best to maintain a detailed feedback between the descriptive morphological work and the functional analysis, be it direct observational or inferential. It is possible to miss some morphological attribute or some aspect of the function, but the feedback between the two frequently indicates the missed point. In a redescription of the laryngeal muscles in the American Crow (*Corvus brachyrhynchos*) (Bock 1978), I was unable to formulate a mechanism by which these muscles closed the glottis. Reexamination of specimens reveals that I had completely overlooked a deep portion of the M. constrictor glottidis. This previously undescribed portion could be easily overlooked even in the most careful dissection. In a similar fashion, feedback should be maintained between work on the form-function complex and the field study of biological roles and interactions with selection forces. This feedback permits both groups of workers to look for details that can be overlooked. In study of the adaptive radiation of the Hawaiian genus *Loxops* (Drepanididae) (Richards and Bock 1973), Richards completed his field work on feeding behaviour before dissecting the feeding apparatus. Only then did he discover the asymmetrical jaws and jaw muscles of *Loxops coccinea*. The form-functional analysis demonstrated that these birds experience strong laterally directed forces acting in opposite directions on each jaw. We developed an adaptive hypothesis for the asymmetrical jaw apparatus of the species based on hints from the field observations, but were unable to test the hypothesis with subsequent field observations. Unfortunately it is not possible to have feedback between these several parts of adaptational analysis in many studies, in which case the morphologist dissecting museum specimens must exercise special care. In a study of the sublingual pouch of Clark's Nutcracker (*Nucifraga columbiana*), information was constantly exchanged between the laboratory and the field workers, allowing ongoing tests of hypotheses arising in both parts of the study (Bock *et al.* 1973).

VI. IMPORTANCE OF ADAPTIVE INFERENCE IN MUSEUM RESEARCH

Demonstrations of individual adaptations, of adaptive evolutionary changes, and of adaptive radiations are most interesting contributions to biology in their own right, but these conclusions and the work leading to them are equally important to other studies based on museum specimens. I would like to discuss three areas of such work and finally to discuss the relevance of adaptive inference to general evolutionary theory.

Ecologists have always turned to museum specimens to obtain various categories of information for the development and testing of ecological theory. For the past two decades, a field of ecomorphology has developed. It is characterized by the use of multivariate statistical techniques using sets of relatively simple morphological variables. The variables are usually rectilinear measurements on bones or body parts (body, wing, tail, bill, leg, *etc.*). Often only a few variables are measured (less than 10 in some studies), and a small number of individuals per species are used. The results of the analyses are used in different ways. Karr and James (1975) and Ricklefs and Travis (1980) used principal components analysis, based on a small number of measurements taken on the study skins of birds, to describe a morphological space which they assume is congruent with ecological space. The inferred ecological space was used to inquire into questions of community organization. A second approach has been to compare the radiation of different taxa (Keast 1972). A third approach is to uncover different adaptive complexes in closely related species of birds (Leisler 1977, 1980; Leisler and Thaler 1982). Reviews of these several approaches in ecomorphology have been published by James (1982) and Leisler and Winkler (1985), and critiques by Wiens and Rotenberry (1981) and Wiens (1982). It should be noted that these approaches to ecomorphology depend heavily upon the use of museum specimens, both taxonomic and morphological, for morphological measurements. Furthermore, these studies assume, often implicitly, that the variables somehow subsume adaptations or adaptive differences.

These ecomorphological approaches suffer from an incomplete analysis of the possible adaptive significance of the features measured, and from the use of unrealistically simple morphological characteristics to analyze complex ecological and evolutionary questions. Moreover, they are based on the

dubious assumption of straightforward congruence between morphometric characteristics and ecological functions (e.g. adaptiveness of the morphological traits), an assumption that is simply not valid (Bock 1977b). The rise of ecomorphology is most important because it attempts a synthesis of morphological, ecological, and evolutionary questions in which the study of museum specimens plays a major role. However, much current development of ecomorphology is based on a series of untenably simple assumptions. Unless careful attention is given to these foundations of ecomorphology and unless future development of this field is placed on a proper footing of adaptive inference, ecomorphology will soon end in a sterile morass of numbers, calculations, and tables.

Classification above the generic level has always been closely associated with morphological analysis of museum specimens. Indeed most morphological research using museum specimens continues to be for systematic analysis of the higher categories. Relatively few of these studies have been founded on adaptive inferences largely because of the training of systematists, not because of any sound theoretical objections to this approach. Systematists have always been concerned with problems of convergence and with independent parallel origin of similar features. Unfortunately these troublesome aspects of taxonomic analysis have too often been confused with the adaptiveness of taxonomic features. Even today one reads expressions such as: *Adaptive features are not useful in systematics*; or, *Features should be divided into a class of adaptive features and a class of phylogenetic features*, with the implication that only phylogenetic features are useful in classification. I have demonstrated that adaptiveness and taxonomic usefulness are two quite separate attributes of features and do not conflict with one another (Bock 1967, 1976, 1981). Basically almost all features used in systematics of the higher categories can be shown to be adaptive. Whether or not they are taxonomically useful is an entirely different matter, and must be shown using other analyses. Moreover I argued that a thorough adaptive analysis of taxonomic features is not only useful but essential to their proper systematic application (Bock 1981). This conclusion belies that of some systematists, mainly the pattern or ordered cladists, who claim that functional-adaptive analyses cannot, in principle, be used in systematic work because of their belief that classification is not based on the known mechanisms and processes of evolutionary change (Cracraft 1981).

Most systematists agree that in some way classifications should reflect the evolutionary history of organisms; this history includes both the pattern of phylogenetic events, including branching, and the rates and amount of evolutionary modification. Clearly much of this evolutionary change is adaptive. Nevertheless, many of the observed morphological differences are paradaptations so that careful attention must be given to the chance-based mechanisms of evolution and their consequences, as well as to the action and results of selective agents. If much of evolutionary history has been shaped by the action of selective agents, and if most of the morphological features used by systematists as taxonomic characters are adaptive, then it follows that taxonomic methods must be based on functional-adaptive analyses. The methods of adaptive inference based on museum specimens outlined in this paper are central to systematic analysis above the generic level. Future progress in understanding the classification of organisms, both fossil and living, depends largely on the application of these methods.

Paleontology, and especially vertebrate paleontology, has always been closely associated with study of anatomical specimens for identification of fossils and for reconstruction of fossil organisms. Much of the work in vertebrate morphology, including functional and adaptational analyses, was done by paleontologists during the first half of this century — indeed paleontologists were mainly responsible for survival of morphology during the great decline of this science in that period. Interest by paleontologists has not decreased since 1950, when morphology experienced a revival characterized by a great growth of interest in functional studies. Without question, paleontologists wish to deduce the functional and adaptive significances of the structures observed in fossil specimens, and to inquire into the possible adaptiveness of evolutionary changes observed in phylogenies of fossil organisms. The problem is what can be done and what cannot be done given the nature of fossil material.

Basically fossil specimens provide information about the skeleton of the organism. Information is available about the conditions of sedimentation, but this says little or nothing about the actual ecology of the organism. Some inferences may be gained of the soft anatomy (e.g. position of muscles from muscle scars), but this information is fragmented and far more limited than usually believed. From observations of muscle scars, and by analogy from the musculature of related living animals, inferences about the existence and position of some, but usually not all, of the muscles can be reached, but little information can be gained about fiber arrangement, fiber length, and fiber cross-sectional area. The size and shape of articular facets provide some indication of the axes of rotation of bones at that articulation and perhaps

some idea of the extent of their movement, but a precise knowledge is not possible in the absence of information about the articular ligaments. Tooth shape and the pattern of wear facets provide a general idea of diet and of the movement of the jaws during chewing. From such evidence, it is frequently possible to reach reasonable functional conclusions, using the inferential methods from observed morphology, about structural features in fossils if they are plausible mechanical functions such as locomotion or jaw movement, or fairly obvious ones such as mechanical protection. Difficulties exist even for seemingly obvious features such as the elongated canines of the saber-toothed cats. And real problems, with perhaps impossible solutions, exist for features such as the elongated dorsal spines of the trunk vertebrae of *Dimetrodon*, the dorsal plates along the back and the sharp spikes at the tip of the tail of *Stegosaurus* (Were they defensive or did they have a role in sexual behaviour?), or the nuchal shield of the horned dinosaurs. The paleontologist must work with the inferential method for determining function and for this reason alone morphologists must perfect the form-function correlations needed in this method. And much more can be done with this method than has been suspected.

Real problems exist in attempts to deduce the adaptive significance of features observed in fossils. Really nothing is known about the ecological factors acting on fossil organisms and the possible selective agents. Statements about biological roles are usually vague and general at best. Because much of the essential information needed to reach conclusions about the adaptive significance of features in fossil organisms is lacking, I conclude that paleontologists are unable to make adaptive inferences except for the most obvious and superficial ones (see Bock 1977b). Consequently, it is not possible for paleontologists to reach conclusions about the adaptive nature of observed changes in the fossil records in almost all cases. In the future, it may be possible to relax the severity of this conclusion if much more is learned about the form-function correlations in fossils and about ecology of these organisms.

Lastly, adaptive inference has a major role in current development of evolutionary theory. Perusal of the history of the "Synthetic Theory of Evolution" (Mayr and Provine 1980) demonstrates that morphologists contributed little to this phase in the history of evolutionary theory, and that almost nothing new was said about concepts of adaptation or of adaptive evolutionary change (see Davis 1949). A few evolutionists have specialized in this area over the past quarter century, but the extensive controversies of the past decade indicate that a broad consensus of ideas on adaptation has yet to be reached. A similar slowness of theoretical development and lack of consensus exist for concepts of macroevolutionary change (see Simpson 1953; Bock 1979) — these two areas of evolutionary thought are closely related.

Many of the concepts directly associated with adaptation have already been discussed; I would like to mention here a few topics that are infrequently considered but are of prime importance. The notion of key innovation has been discussed under several headings such as key mutation (Simpson 1953: 190) and general adaptation (Brown 1958), but usually under terms like evolutionary innovation or morphological innovation (Miller 1949; Bock 1965: 275; von Wahlert 1965; Liem 1973, 1980). A key innovation or a key adaptation is one whose appearance is pivotal for the exploitation of a new habitat and usually central to an adaptive radiation. The cichlid pharyngeal jaw (Liem 1973; Liem and Greenwood 1981) is an excellent example of a key innovation. Simpson suggests that the evolution of key innovations is coupled with a threshold effect (Simpson 1953: 196), but this concept has never been defined carefully and has been rejected by other workers (Bock 1965: 279). I know of no way of recognizing key innovations except in retrospect, and there appear to be no characteristics delineating key innovations from other adaptations except the resulting adaptive radiation. Although this concept has been in general use for a number of decades, no good analysis of key innovations exists and one is sorely needed.

Among the topics included under the general heading of macroevolution, none has caused more difficulty than the conception and recognition of intermediates between two well defined major groups — missing links. If such forms are to be searched for among fossil or living organisms, the evolutionist must have some mental picture — a search image — of these missing links. For a long period following Darwin, evolutionists had visualized these intermediate forms as possessing all traits equally intermediate between those found in the ancestral and in the descendant groups. This idea was based on the concept that evolutionary change proceeded uniformly for all characteristics of the whole organism. A missing link between reptiles and birds, say a form halfway in the evolution to modern birds, would be halfway intermediate in all of its features. The error of this argument was pointed out by de Beer (1954), based on his detailed study of *Archaeopteryx*. He demonstrated that the organism can be subdivided into a number of separate traits, each of which evolves at different times and at different rates. The consequences of this evolutionary pattern is that intermediate forms are a mosaic of ancestral features, descendant features, and

assorted intermediate ones at diverse stages of evolution. This pattern of mosaic evolution stems from the complex and changing pattern of selection forces acting on the phyletic lineage of forms evolving from the ancestral group to the still unknown descendant one. The mosaic of changing features must be integrated into a functioning whole organism which can survive in its particular environment at each stage in the transition from the ancestral to the descendant form. It is not only important to analyze the possible adaptive evolution of each individual feature, but to show how the integrated, mosaic pattern of these separate changes constitutes a viable organism able to survive in its environment at all stages in the macroevolutionary episode (Gutmann 1977, 1981; Gutmann and Bonik 1981). Although the notion of mosaic evolution is central to the analysis of macroevolutionary change, and has been discussed by a number of evolutionists, it was not mentioned at all in a review of the question of missing links (Olson 1981). Mosaic evolution is central to the study of adaptive change in macroevolution. Notwithstanding the careful presentation by de Beer and others, it deserves additional study and analysis of additional examples. Of special importance are the integration of the differentially evolving features into functional whole organisms which can survive in their environment, and the breakdown of the pattern of mosaic evolution as one goes from the whole organism or from complicated functional complexes of features down to unit features. Clearly as one approaches a unit of morphological feature, the phenomenon of mosaic evolution disappears. Success in the study of a phenomenon of macroevolution, such as mosaic evolution, depends strongly on proper adaptive inferences of individual features.

Generalized and specialized are terms commonly used by evolutionists as adjectives describing particular properties of species and their traits. Most workers seem to have at least a rough idea of what these terms mean. As applied to adapted features, generalized implies that the feature permits interaction with a broad spectrum of ecological factors and their selection forces, and specialized just the opposite. Yet these terms are often applied to features after a study of only their morphological form, with specialized used for those structures exhibiting an extreme development, whatever that means. Moreover, the implication exists that generalized features are primitive ones, or at least ones that will permit further adaptive radiation of the group, while specialized features are characteristic of more advanced species within a group which are now in an evolutionary cul-de-sac. These conclusions are not valid as pointed out by Amadon (1943).

I do not know of any decent analysis of the notion of generalized/specialized features. Any such treatment is dependent on a proper understanding of adaptation and an adaptive analysis of a broad range of features.

Adaptive inference continues to be of major importance in studies using museum specimens for its own sake and for other museum-related work in biology. Unfortunately, the facilities and training needed for excellent museum research in adaptive inference have not kept pace with developments in other areas of museum investigation. This shortcoming is partly the consequence of a mistaken belief that suitable adaptive inference can be done simply on the basis of casual morphological examination. Hopefully, with increasing realization of the need for detailed knowledge of the form and functions of features, of ecological factors, and of the interaction between organismal features and environmental factors as minimum prerequisites for adaptive inference, facilities, training, and standards for this area of museum research will be improved. The outcome will be broadly advantageous for many areas of systematic and evolutionary biology.

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11. MUSEUM COLLECTIONS AND THE STUDY OF ANIMAL SOCIAL BEHAVIOUR

E.H. Miller

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I. INTRODUCTION

Traditional zoological collections in museums seem like unlikely material to enhance our understanding of animal social behaviour. Thus it is not surprising that zoological research in museums made little or no direct contribution to the rise and development of ethology and comparative psychology. Despite this apparent independence, early comparative research on behaviour emphasized evolutionary concepts that were derived from traditional comparative zoology, much of which was carried out in museums. Furthermore, much behavioural research was concerned with stereotyped motor patterns used in visual displays of birds and fish, and these motor patterns often served to accentuate striking colours, patterns, or special structures — features whose adaptive significance had long been unclear (though vigorously debated). Thus, studies on animal behaviour developed through comparative methods and evolutionary thinking which were widely used by museum zoologists, and quickly provided understanding of the functions of many morphological attributes of organisms, which was important to museum workers.

The relationships just outlined reflect the interdependence of morphology and behaviour, and the fact that behaviour is a component of phenotype and can be treated and analyzed as such by evolutionists and systematists. The relationships of morphology to social behaviour are less well understood than to individual behaviour and ecology, because the latter are often reflected in mechanical efficiency of parts, or in close functional adaptation to identifiable selective agents like temperature or food (e.g. Reimchen 1983). In contrast, many morphological features involved in social behaviour seem unnecessarily complex for the purposes they serve, and sometimes even appear disadvantageous [e.g. the massive antlers of the Irish Elk (*Megaloceros giganteus*), the plumage of male Birds of Paradise (Paradisaeidae)]. Such characteristics partly reflect the complexity of evolutionary responses to sexual selection and other forms of social selection; (see section II.A and Payne 1983), and are poorly understood because of this, and because of the dearth of research on form and function in social morphology. I develop this point below, with particular reference to communication, sexual selection, social systems, and reproductive challenges between related species (section II).

If more research of a unifying and comprehensive nature is required, we should expect and welcome changes in the rationale for scientific collecting and in the nature of specimen preparation, a point reiterated below (section III.A). Even specimens collected and prepared in non-traditional ways are inadequate for future museum collections, whose aim should be to store as much potential information as possible. Auxiliary collections focussing on behavioural events should be encouraged, and museums are a natural repository for them: audio recordings; movie films; and photographs (section III.B). These sorts of collections also point to certain collecting priorities, collecting techniques, and research needs.

Museums have research and curatorial roles set by traditions and by existing collections. Research roles should expand to use collections more innovatively, and to promote collecting which is both scientifically timely and fulfills the museum's role as a scientific and cultural storehouse. I conclude this chapter with a consideration of these views (section IV).

II. EFFECTS AND INFERENCE

In this section, I will explore chosen topics which are relevant to the use of collections in research on animal social behaviour. Some of the examples are based on museum specimens; others are not, but illustrate social processes and morphological effects which could be explored with such material.

A. Communication and Social Systems

1. Sexual Differences In Size

Size differences are a widespread form of sexual dimorphism. These have been documented for many species, and are standard parts of diagnostic treatments, original descriptions, and taxonomic reviews. Understanding of the social significance of sexual size dimorphism has lagged far behind documentation of it, though such dimorphism is often related in a surprisingly simple way to social attributes across species, including aggressive, mating, and parental behaviour.

Some early studies established broad patterns of correlation between sexual size dimorphism and mating systems across species. For example, males are substantially larger than females in those species of Phocidae (seals) and Otariidae (fur seals and sea-lions) which aggregate to bear pups and mate on land. In contrast, species with more aquatic social systems and lower levels of polygyny (or even monogamy), show moderate or even reversed sexual dimorphism in size (Bertram 1940). This simple trend reflects the importance of strength and large size in male combat, the outcome of which determines access to oestrous females (reviews by Bartholomew 1970 and Stirling 1983). An additional mating advantage to large size in many taxa lies in the ability to sequester or physically overpower females. Forced insemination is the rule in semiaquatic and bottom-walking species of turtles, and males are at least as large as females in the great majority of them. In contrast, terrestrial species are characterized by male combat over access to females, and as expected this group also tends toward size dimorphism in favour of males (Berry and Shine 1980). Similar trends exist for snakes and amphibians (Shine 1978, 1979), primates (Crook 1972; Leutenegger 1978, 1982), and many groups of birds (Selander 1972), but are not always easily interpreted (e.g. Bährmann 1976; Andersson and Norberg 1981; Johnston and Fleischer 1981; von Schantz and Nilsson 1981; Price 1984).

Sexual differences in size of body parts also abound. Canine teeth of many primate species are larger in males than females, but significantly less dimorphism occurs in monogamous species than in those with other kinds of mating systems (Harvey *et al.* 1978; see also Leutenegger and Kelly 1977, and Leutenegger 1982). This trend indicates the importance of direct male combat with use of the canines in many species, though ecological factors (notably predator pressure) are also involved (Harvey *et al.* 1978).

Body size is intricately bound to nutritional plane, developmental events, and other proximate factors, many of which must signify an individual's phenotypic and genotypic "quality," hence is a good predictor for its ability to defend a social group against predators, or to invest directly in the production or rearing of young (Alexander 1974; Trivers 1976; Borgia 1979; Andersson 1982a; Wasser 1983). Therefore, body size could be expected to provide important cues to contestants appraising one another in aggressive interactions, and to females (especially) and males when choosing mates. Such social processes cannot be inferred from trans-specific trends like those summarized above, but demand detailed field studies of populations.

Field research on several species of digger wasps (*Philanthus*) has established that territorial resident males are larger than most males in the local population, including those replacing residents that are removed experimentally (O'Neill 1983). This suggests either that only large males mate, or that non-territorial males of smaller size employ alternative reproductive tactics. The latter suggestion has been developed for insects by Alcock (1979), who distinguished several classes of behavioural variation based upon whether variants are syntopic or synchronous. For present purposes, it is sufficient to note that alternative (or continuously varying) tactics may coexist in a population, and so may the phenotypic correlates of such behavioural tactics; Thornhill and Alcock (1983) provide a trenchant review (see also Alcock 1984). Other studies have repeatedly revealed the advantage of large size in direct physical competition for mates, and that size is an important cue in assessment during aggressive encounters (e.g. Miller 1975; Riechert 1978; Thornhill 1984). Understanding of the relationship of mechanisms of mate-choice to sexual dimorphism is much poorer, though assortative mating on the basis of body size is known for several species in which choice of mate is important (Jehl 1970; Ankney 1977; Thornhill and Alcock 1983).

Linkages between general patterns of sexual size dimorphism and social systems can be revealed solely by museum research, using an interpretive framework provided by behavioural ecology and sociobiology. It is impossible to infer social processes at a much finer level, however, because of the diversity of selective pressures which promote sexual dimorphism in size (direct combat, ecological differentiation, parental role differentiation, etc.) and in size variation (alternative mating strategies, ecological amplitude, etc.). At this level of understanding, analysis of sexual size dimorphism demands statistically adequate samples, and interpretation demands naturalistic studies to reveal behavioural correlates of size. A second and complementary point must be made: body size alone must rarely determine reproductive success, especially considering the large number of important intrinsic and extrinsic factors which contribute to choice of mate and reproductive opportunities (e.g. Brown and Downhower 1983). Many behavioural, ecological, and morphological attributes of males have been studied in the polygynous Red-winged Blackbird (*Agelaius phoeniceus*), but the most prominent finding is the high spatial and temporal variability of factors which lead to breeding success (Searcy and Yasukawa 1983). In a species of pupfish (*Cyprinodon pecosensis*), territorial males show considerable variation in the number of females with which they mate: in one study, topographic complexity of the territory accounted for up to about 65% of the variance in male reproductive success, and colouration another 13%; male size and behaviour together accounted for less than 2% (Kodric-Brown 1983). Clearly, the appropriate place to test many hypotheses about ultimate causes of sexual differences in size is the field.

2. Differentiation in Social Roles

Individual animals are unique in their social behaviour, but are organized collectively as subgroups in many animal societies (Wilson 1975; Brent 1978). Behavioural characteristics of individuals can be quantified and analyzed multivariately, to reveal subgroup differentiation (Dudzinski and Morris 1970; Deitchman *et al.* 1979). This approach has been used effectively in investigations on behavioural role structure in primate societies, and has demonstrated some congruence between social roles and phenotypic characteristics (age, gender, dominance: Sade 1972; van Hooff 1975; Fairbanks *et al.* 1978; Gage and Lieberman 1978; Strayer and Harris 1979; see also Williams *et al.* 1972, and Rhine and Westlund 1981). However, the only detailed study of correspondence between morphological and role-behavioural characteristics in vertebrates is that of Brown *et al.* (1982), to my knowledge. Social insects provide most insight into complex social structure and its relationship to individual morphology. Detailed observations on adult females of a primitively social bee, *Lasioglossum zephyrum*, are instructive. This species has weakly developed social behaviour, with nesting colonies averaging only about 14 females (many females even nest solitarily). In addition, castes are difficult to define on morphological grounds. Using various characteristics of interactive and care-giving behaviour, Brothers and Michener (1974) documented some behavioural differentiation suggestive of roles, and behavioural specializations of the bee with the largest ovaries in each colony, justifying her designation as queen. Similar research has been carried out on the morphologically undifferentiated individuals of a paper wasp (*Ropalidia marginata*) with comparable results (Gadagkar and Roshi 1983).

Physical and behavioural caste specialization are most pronounced in termites (Isoptera) and certain groups of ants (Hymenoptera) (Wilson 1971; Oster and Wilson 1978; Lenoir and Ataya 1983). The terms

polymorphism and polyethism have special meanings in social insects, as the coexistence of two or more morphological and behavioural castes (respectively) within the same sex. Polymorphism is apparently always accompanied by behavioural specialization, but the reverse does not always hold (see further). In ants, the soldier caste often shows extreme morphological and behavioural specializations, particularly of the head and mandibles. A shearing function occurs in some groups, directed at cutting integument and appendages of enemy arthropods; piercing occurs in others, through the use of pointed and sickle- or hook-shaped mandibles; and blocking of entrances to nests is another, involving the shield- or plug-shaped head (Fig. 1).

In extreme cases like those mentioned, some broad patterns of polyethism can be inferred from knowledge of polymorphism, but inference weakens as polymorphism becomes weaker or less specialized. For example, a moderate degree of polymorphism characterizes the fire ant *Solenopsis invicta*, but samples of workers engaged in various behaviours do not always differ significantly from one another in body size (Wilson 1978).

The difficulty in inferring behavioural from morphological characteristics can be appreciated from a model postulated by Wilson (1976). The model concerns the relationship of behavioural responsiveness to age in ants. One hypothetical extreme has different-aged ants responding differently to tasks such as feeding larvae, dealing with misplaced eggs, and so on (model 1 in Fig. 2). As the number of tasks is increased, the distinction between adjacent age groups (temporal castes) becomes less clear, and the caste system becomes essentially continuous. A contrasting alternative specifies concordance between various response curves, so that the same ensemble of workers attends to more than one task. As the number of tasks grows, the number of castes still remains low, resulting in a more discrete caste system (model 2 in Fig. 2). Wilson (1976) refers to this process as *behavioural discretization*, and it bears no simple predictable relationship to morphology. In a subsequent paper, Wilson (1978) introduces the concept of *alloethism* as an analogue to allometry: the behavioural attributes as a function of size.

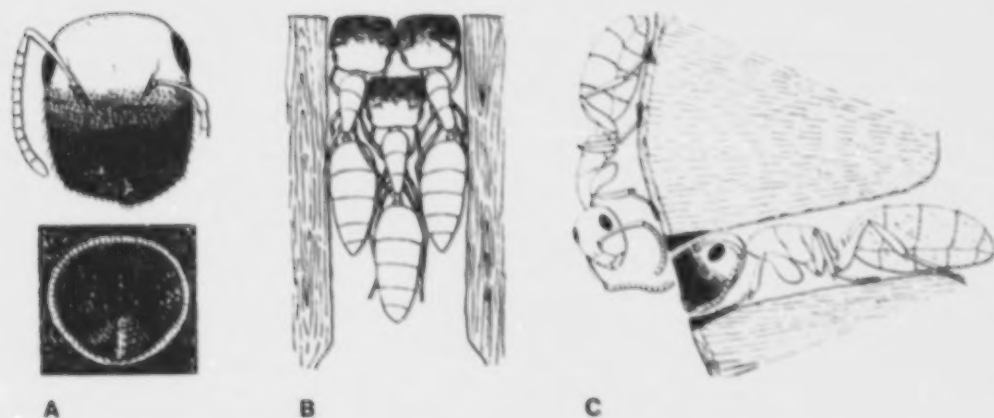
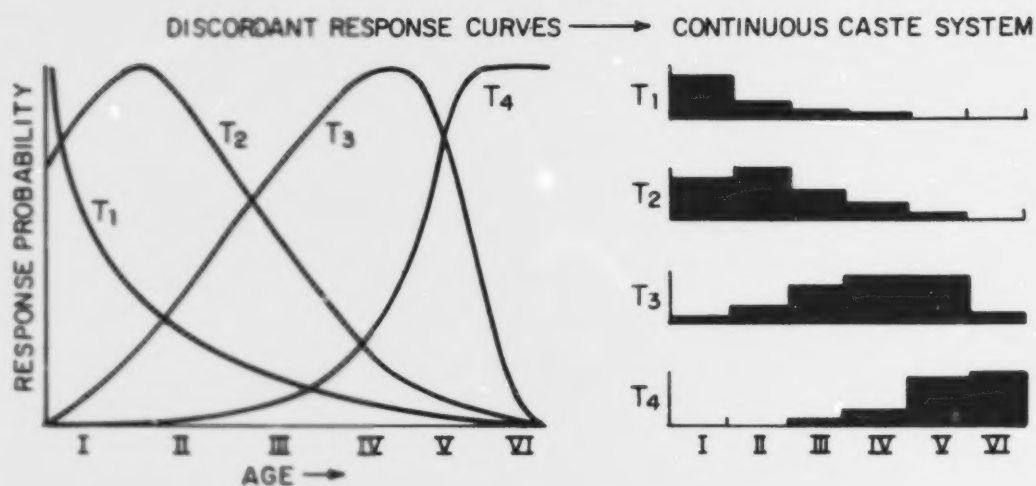


Fig. 1. Head morphology and nest-guarding behaviour by soldiers of the European ant *Camponotus truncatus*. A, Two views of the head, the bottom one being a frontal view framed by a small circular entrance to the nest, demonstrating how the head serves to block the entrance. B, A group of workers communally plugging a large entrance. C, A minor worker approaches a soldier that is blocking a nest entrance. (After Fig. 8-17 of Wilson 1971.)

MODEL 1



MODEL 2

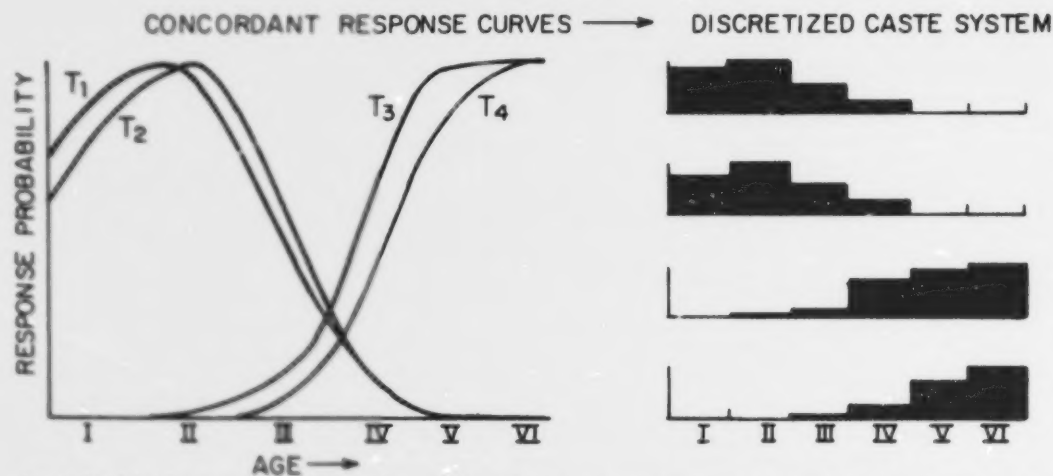


Fig. 2. Models of extreme alternatives in the evolution of temporal castes in ants. Age of workers is divided arbitrarily into six periods (I-VI). In model 1 (upper), worker responsiveness to four tasks (T_1 - T_4) develops strongly out of phase. Consequently, each of the four tasks is handled by a distinct ensemble of age groups (temporal castes), which are represented by size-frequency distributions on the right. If the number of tasks increased, overlap among age-group ensembles would increase correspondingly, and would eventually approach a continuous transition. In model 2 (lower), the response curves are clustered into groups that are approximately in phase, resulting in more than one contingency being addressed by single age-group ensembles (castes). In this example, two ensembles perform two tasks each. Even if the number of tasks increased greatly, the number of ensembles would remain small. (From Fig. 1 of Wilson 1976.)

3. Special Structural Features

Ethology and neurophysiology have revealed numerous examples of exquisite adaptations to social life in features of morphology, physiology, and behaviour. Some of the best documented examples concern peripheral filtering and selective responses to species-specific signals, as in anurans (Capranica 1976) and insects (Elsner and Popov 1978). Morphological correlates of many such systems cannot be appraised on most museum specimens of mammals and birds, because adaptations are at the level of integrative functions in the central nervous system (Newman 1978). However, morphological adaptations in sensory structures abound, as exemplified by the simple relationship of pheromonal sensitivity to length of antennal receptors (sensilla trichodea) in male cabbage loopers, *Trichoplusia ni* (Fig. 3; O'Connell *et al.* 1983). Such examples of close adaptation between signals and receptors could be multiplied. However, the main point that emerges is simply that full understanding of the mechanical and neurophysiological relationships of sensory structure and function requires detailed descriptive and experimental research. Much of the latter is not appropriately coupled to research on museum collections, and cannot usually be used to set procedures of specimen collection or preparation (section IV).

Specialized structural features that are more easily studied on museum specimens, and that provide suitable material for field research, include those involved in combat or signal emission. Prominent among these are patterns and other optical characteristics of pelts and skins, specialized appendages such as horn-like organs, and other tegumentary modifications like crests, manes, *etc.* (Fig. 4; Geist 1966, 1971; Eisenberg and Gould 1970; Andersson 1982b; Wemmer and Wilson 1983). Characteristics and variation of such structural features can be rigorously described and quantified on the basis of museum material, and trans-specific trends can be delineated (*e.g.* Guthrie 1971). However, broader appreciation of the evolutionary significance of signal morphology must come from observations or experiments with living animals, because motor patterns that are involved in communication are typically highly specific to species, and even to population (Colgan 1983). Furthermore, motor patterns can reveal major evolutionary trends in ritualization, that can only be hinted at on the basis of morphology. Finally, knowledge of orientation and many other facets of signalling behaviour is essential to understanding the behavioural, ecological, and evolutionary significance of signal morphology (Hailman 1977a, b). Threatening behaviour in horned or antlered ungulates provides many examples. In the Bovidae, horns are the major weapons, and these show great variation in structure and use among species (Fig. 4). Behavioural variations in fighting styles have led to striking differences among species in the expression of threat. For example, Wildebeest (*Connochaetes taurinus*) drop to their "knees" in fighting, and Ibex (*Capra hircus*) rise preparatory to striking downward; in both cases, initial movements of fighting have been ritualized as symbolic expressions of threat (Fig. 5; Walther 1974, 1977).

Other widespread structural features whose functional and evolutionary importance are unclear from museum specimens are those involved in sound production. For example, male wolf spiders (*Schizocosa ocreata*) have a stridulatory organ at the palpal tibiotarsal joint, and conduct sounds to the substrate by the stout spines at the distal ends of the palps (Rovner 1975). Understanding of the mechanism of sound communication, and of the species-distinctive characteristics of the sounds (Stratton and Uetz 1981), relied on joint studies of structure and function. A final example concerns an aquatic insect, the waterboatman *Palmacorixa nana*. Both sexes "produce sound by rubbing fields of pegs on the inner surfaces of the prothoracic femora ... over thickened flanges of the maxillary plate;" males have a second stridulatory structure, consisting of about 33 pegs along the inner face of each mesothoracic femur — these are drawn across the edges of the female's hemelytra during mounting and copulation (Aiken 1982:55).

The importance of studies on living animals to understanding the function of morphological features cannot be stressed too much. For example, only through such research has a glimmering of understanding been achieved of the behavioural significance of the bizarre, fleshy snout hump in the Gharial (*Gavialis gangeticus*) (Fig. 6; Whitaker and Basu 1982) — a feature whose mere existence was doubted until recently (Neill 1971; Gore 1978)!

4. Social Systems, Growth, and Ecogeographic Variation

Social selection can have rapid and striking effects on those components of phenotype contributing to mating success, particularly when variance in success is high (Payne 1979). This is the major reason for

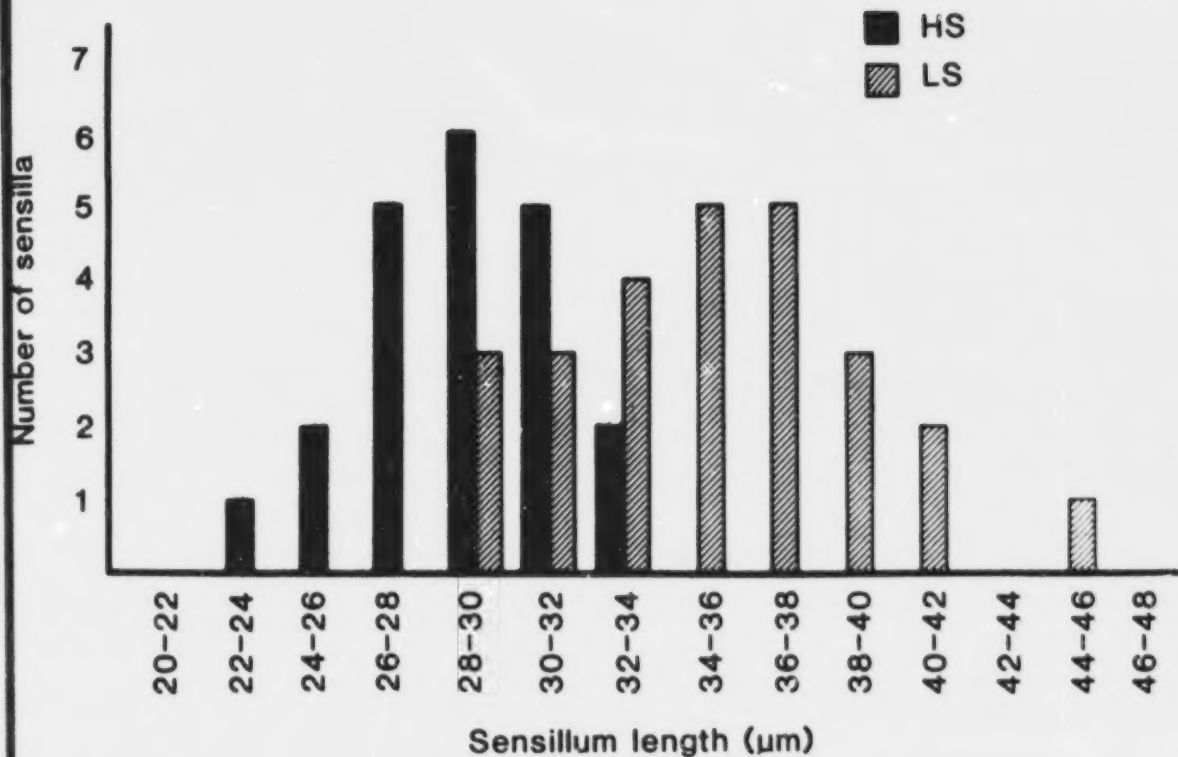


Fig. 3. Frequency distribution of the length of pheromone-sensitive sensilla trichodea in the male cabbage looper (*Trichoplusia ni*). Sensilla with high (HS) and low (LS) spontaneous activity are distinguished. Receptor neurons associated with HS sensilla are only excited by large amounts of pheromone, and LS by small amounts. (From Fig. 2 of O'Connell *et al.* 1983.)

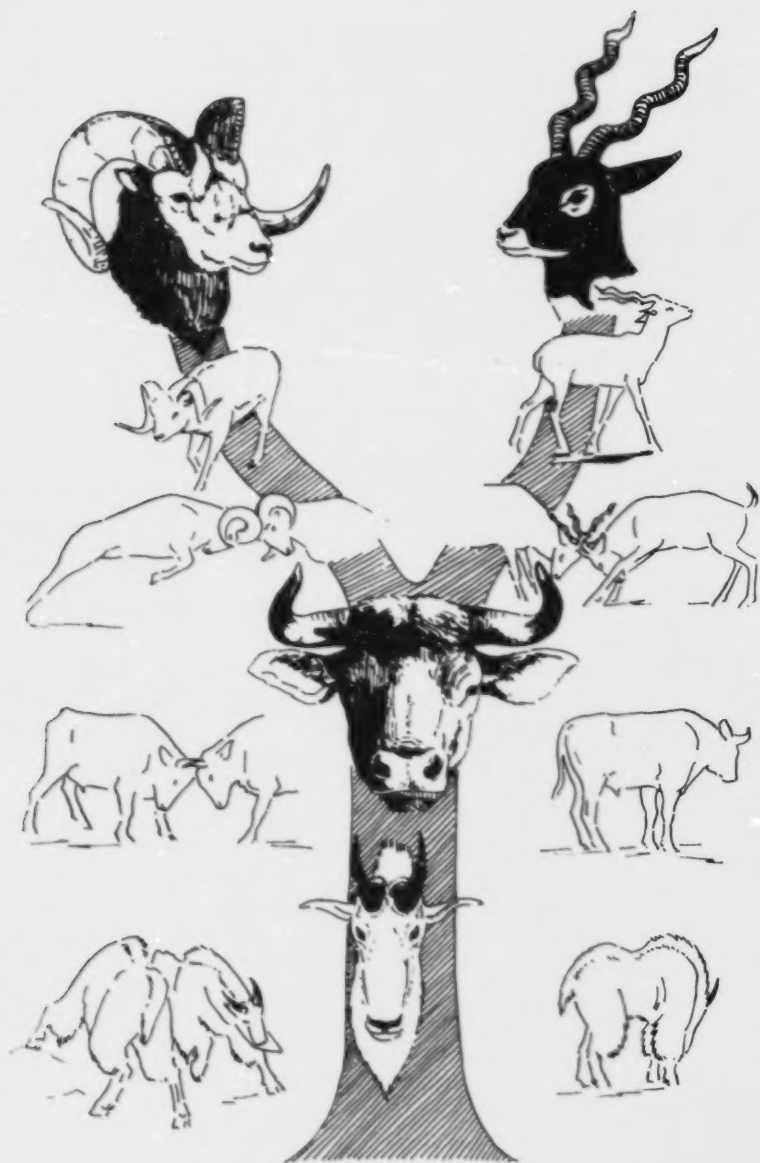


Fig. 4. Hypothetical trends in the coevolution of horn structure, and of behaviour involved in fighting and optical communication. The primitive horns are short and sharp, and the skull thin and fragile. Combat takes place in lateral orientation, and broadside displays are prominent (e.g. *Oreamnos*, bottom). Next, head-to-head combat evolved as a defense mechanism. The skull is heavy, and horns curve out to hold the opponent when in combat. Broadside display is prominent (e.g. *Bos*). From the style of frontal engagement, two forms of combat evolved: "wrestlers" illustrated on the right (e.g. *Antelope*); and "rammers" shown on the left (e.g., *Ovis dalli*). In wrestlers, combat is a frontal pushing match, and broadside display is prominent. In rammers, the large horns serve as a weapon and a guard, and have an important display function; no broadside display occurs. (From Fig. 15 of Geist 1966.)



Fig. 5. Ritualized threat postures in two species of Bovidae, the Wildebeest (*Connochaetes taurinus* - A), and the Ibex (*Capra hircus* - B). (From Fig. 5 of Walther 1974 and Fig. 10 of Walther 1977.)

the evolution of elaborate adornments and weaponry in numerous species, particularly polygynous, promiscuous, or polyandrous ones. The general aspects of this correlation are well established but, as with topics discussed above, full understanding of the relationship demands integrated research.

An example which illustrates this point concerns egg size in shorebirds. Species-typical egg dimensions for shorebirds were documented long ago, but evolutionary explanations for the differences among species awaited a comprehensive analysis using information about mating systems. Such a study revealed a simple relationship of egg size to mating pattern: eggs are small relative to female size in all species except single-clutched, monogamous ones, a correlation that fits well with theories on parental investment (Ross 1979; Erckmann 1983). Many relationships among mating systems, sexual selection, morphological features, and life-history characteristics may be understood only in the light of demographic data (see Chapter 13). Such data have been used to test hypotheses about sexual size dimorphism in several groups of birds; specifically, is increased size dimorphism (resulting from sexual selection) accompanied by decreased survivorship? Data at the species level have produced equivocal results, but several cross-species examinations have revealed lowest male survivorship in species with greatest size dimorphism (Wittenberger 1978; Searcy and Yasukawa 1981).



Fig. 6. Old print of a Gharial (*Gavialis gangeticus*) showing the fleshy nasal hump which was considered to be imaginary until recently. (From Neill 1971, Fig. 159; compare Gore 1978: 98-99.)

Other links between social selection and features of museum specimens are more direct. In acalyptate flies, sexual signalling and accompanying morphological specializations are very simple in species characterized by resource-based, male-controlled mating systems. More highly developed signalling specializations occur in species where mating decisions by females are important, with the most extreme developments in lekking species (Burk 1981). The relative importance of intra- and intersexual selective pressures moulding secondary sexual characteristics cannot be inferred even from general knowledge of a mating system, however. For example, interactions among male Goldie's Bird of Paradise (*Paradisaea decora*) on the lek may establish a dominance hierarchy before females arrive to mate; mate-choice may therefore not have contributed significantly to the evolution of the striking characteristics of male nuptial plumage in the species (Le Croy *et al.* 1980; see also Payne 1983). Clearly, in this and the preceding examples, detailed field observations are mutually complementary to museum studies of trends within and among species.

Some of the most intriguing variations among museum specimens are attributable to development. Variations of particular interest to ethology concern morphology related to signalling, as well illustrated in birds. Many species of birds show deferred development of male plumage, so that full plumage may not

be acquired for several years. There are two main competing explanations of this phenomenon. One suggests that year-old males should defer breeding effort, because reproduction entails some risk of mortality; this is likeliest in species which exhibit increasing fecundity with age (Wiley 1974). The other suggests that first-year birds are mimicking female plumage, thereby gaining access to high-quality breeding areas where they can establish territories, which are then maintained through site-dominance (Rohwer 1978; Rohwer *et al.* 1980). To date tests of hypotheses pertaining to these explanations have not strongly supported either of them (Rohwer and Niles 1979; Procter-Gray and Holmes 1981; Rohwer 1983). Another example of behaviourally significant variation with age is the checkered white butterfly (*Pieris philodice*). Males invest substantially in their offspring through nutrients passed to the female during copulation, so are under selective pressure to choose young females as mates. They do so partly on the basis of ultraviolet reflectance of wing surfaces, which increases with female age (Rutowski 1982).

Temporal and spatial variations in morphology are widespread. Many are under short-term physiological control, and impossible to deal with using museum specimens (*e.g.* changes in visual appearance by displaying fishes and cephalopods; Morris 1958; Barlow 1963; Moynihan and Rodaniche 1977). Longer-term physiological changes, such as facial colour of patas monkeys (*Erythrocebus patas*) during pregnancy (Loy 1974), and sexual swellings in primates (Dixon 1983), are also impossible to study with museum specimens. Such characteristics are important for fully understanding the adaptive relationships of social morphology to environment, however; thus coloured genitalia form part of a complex system of optical communication in savannah primates, but not in many other groups (Bolwig 1978). The appearance and behavioural use of soft parts are important to describe in field research in general; good examples are Drent's (1965) study on Pigeon Guillemots (*Cephus columba*), with observations on open-mouth displays which exhibit the bright red mouth lining, and Kunkel and Kunkel's (1975) study of species differences in palate pigmentation in estrildid finches.

Mammalian skin glands show extensive variations within and among species. Kangaroo rats (*Dipodomys*) possess a specialized dorsal skin gland, the structure of which has been described in detail by Quay (1954). The size (area) and secretory activity of the glands are easily estimated in museum skins. In *D. merriami*, glandular area and activity are strongly correlated, both being maximal in males during the breeding season (February-June); size and activity in females are much less, and exhibit no seasonal trends (Fig. 7A, Quay 1953). In striking contrast, certain other species show no sexual differences in glandular area or activity, and one (*D. heermanni*) has an annual cycle of area/activity which differs markedly from that of *D. merriami* (Fig. 7B).

Another example of seasonal change in mammals which is related to social behaviour is the American Bison (*Bison bison*). The hair covering the head, beard, and pantaloons, which is best developed in mature males, becomes much shorter following the breeding season. This may facilitate a change in social role from "an aggressive competition toward that of a socially neutral conspecific," thus reducing unnecessary and costly strife when energy storage before winter, and co-existence during winter, are important (Lott 1979:74).

Geographic (subspecific) variation may occur in dorsal glands of *Dipodomys ordi*, as it apparently does in the tundra vole, *Microtus oeconomus*. In the latter species, hip glands are well developed in both sexes at high latitudes, but are best developed only in old males at lower latitudes (Quay 1968). The social-behavioural significance of Quay's observations has not been evaluated in field or laboratory studies. The most detailed analysis of ecogeographic variation in a signalling structure is on facial features of the Steller's Jay (*Cyanocitta stelleri*), a resident west-coast species that breeds from Alaska to Guatemala (Brown 1963). Optical characteristics which are important in short-range facial-visual communication include the crest and facial markings. Lengths of certain markings and of the crest vary in a complex manner throughout the species' range. However, openness of the environment in which short-range encounters occur may be the major influence promoting crest development. Openness is probably related to population density, which further increases the importance of facial-visual communication, partly through relationships with food supply (see Fig. 5 of Brown 1963).

5. Concluding Remarks

The preceding sections all underscore three points relating to collections and collecting. First, myriads of attributes of museum specimens demand explanations that can only come from field research. Indeed, field studies on behaviour coupled with museum research should often be carried out together,

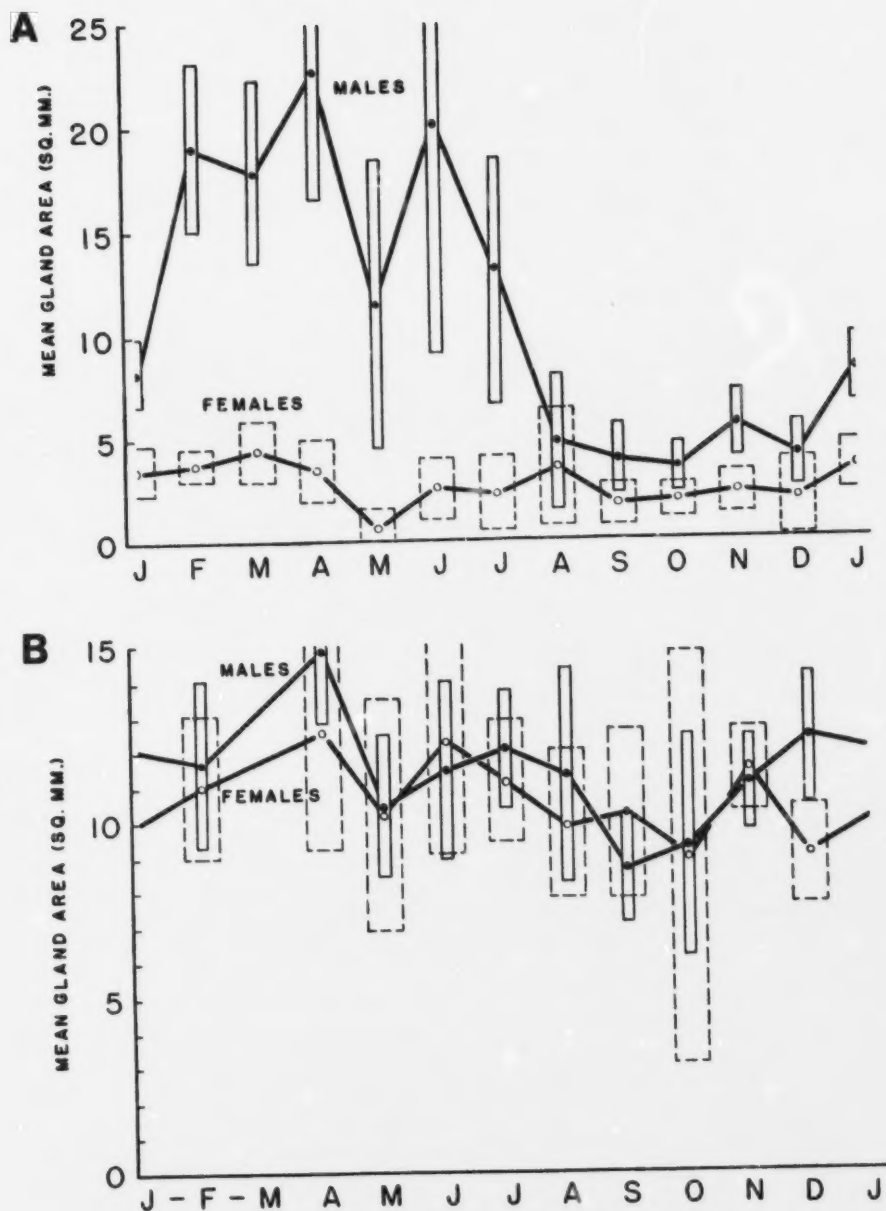


Fig. 7. Seasonal trends in size of the dorsal skin gland in kangaroo rats, *Dipodomys merriami* (A) and *D. heermanni* (B), as estimated from museum specimens. Mean estimates $\pm$ 2 S.E. are shown for each month; months are indicated on the horizontal axis. (After Fig. 1 (lower) and Fig. 3 (upper) of Quay 1953; reproduced by permission of the American Society of Mammalogists.)

and observations in each arena suggest hypotheses which can be tested in the other. For example, patterns of variation in the crest and facial markings of Steller's Jays suggest hypotheses about communication which can only be tested in the field. Similarly, extensive intraspecific variation in winter plumage of Harris' Sparrow (*Zonotrichia querquedula*), and interspecific variation in mammalian rump patches, suggest hypotheses which demand field studies of behaviour (Guthrie 1971; Rohwer 1982; see Fugle *et al.* 1984). Conversely, behavioural attributes have often led to investigations of structure: e.g. infrasound production and laryngeal anatomy in baleen whales (Balaenopteridae) (Sukhovskaya and Yablokov 1979); sound production and tail-feather structure in snipe (reviews by Rutschke 1976; Reddig 1978; Tuck 1972); and structure and function of the "nasal balloon" in male Hooded Seals (*Cystophora cristata*) (Berland 1966).

Second, more information and documentation should accompany specimens. Related to this, specimens should be prepared in ways that meet needs for comparative studies using the millions of museum specimens which already exist, while simultaneously being as complete as possible for other, newer kinds of research. Thus, the habitat, habits, and appearance of many specimens should be written about and photographed more routinely (see section III.B.1, and Chapter 13); and body parts of particular significance for social behaviour (e.g. signal-emitting structures) should be altered as little as possible during preparation, or should have samples routinely set aside for purposes of dissection or histological examination.

Third, collecting needs should be set in light of how adequately existing collections represent socially significant variation. A large collection of Harris' Sparrows which does not include winter specimens, for example, is clearly lacking materials of great behavioural and evolutionary significance.

B. Interspecific Processes

Behavioural interactions among species are common during interspecific territoriality, in various activities in mixed-species groups, or while signalling in complex faunas, when interference can be high. Over longer periods of time, interspecific behavioural interactions must often have promoted species-distinctiveness in mating behaviour and related morphological features (but see Miller 1982, Robertson and Paterson 1982, and Payne 1983).

Selective pressures related to the points just mentioned place a premium on either convergence or accommodation among species (Endler 1981 reviews many relevant aspects of mimicry). Convergence in behaviour and signalling morphology has occurred rarely among species that are interspecifically territorial (e.g. Rohwer 1973), but is clearly expressed in certain mixed-species feeding flocks in Central and South America (Moynihan 1962, 1968; Cody 1969). Interspecific territoriality and other forms of direct interaction among species often simply lead to learned responses which mediate coexistence, or to sharpened discriminatory abilities, without apparent structural changes.

Correlated structural and behavioural changes typically accompany speciation, and are sometimes enhanced in areas where related species coexist. For example, patterns of wing pigmentation in the dragonflies *Calopteryx maculata* and *C. aequabilis*, important to species discrimination by females, are more different in sympatry than allopatry (Fig. 8). Other sorts of evidence also point to the importance of reproductive interactions among species in promoting species-distinctive morphology; for example, intergeneric hybrids in certain families of birds are surprisingly common relative to interspecific hybrids (Banks and Johnson 1961; Parkes 1961, 1978).

Genitalia are often structurally complex and highly species-specific. The phallus of microtine rodents exemplifies these characteristics. Much intraspecific variation in morphology of the phallus and baculum may be related directly to local microtine species diversity, which promotes complexity and low variation to enhance reproductive isolation (Patterson and Thaler 1982; Patterson 1983). Reproductive characteristics in general are profoundly affected by sexual competition, whose evolutionary role in promoting phallic morphology is not well understood, so the proposed relationship remains unconfirmed (see Robertson and Paterson 1982).

As in so many of the examples discussed in this chapter, museum specimens can provide detailed information about structure, but the testing of evolutionarily relevant hypotheses rests on further collecting, or on field or laboratory observations of living animals.

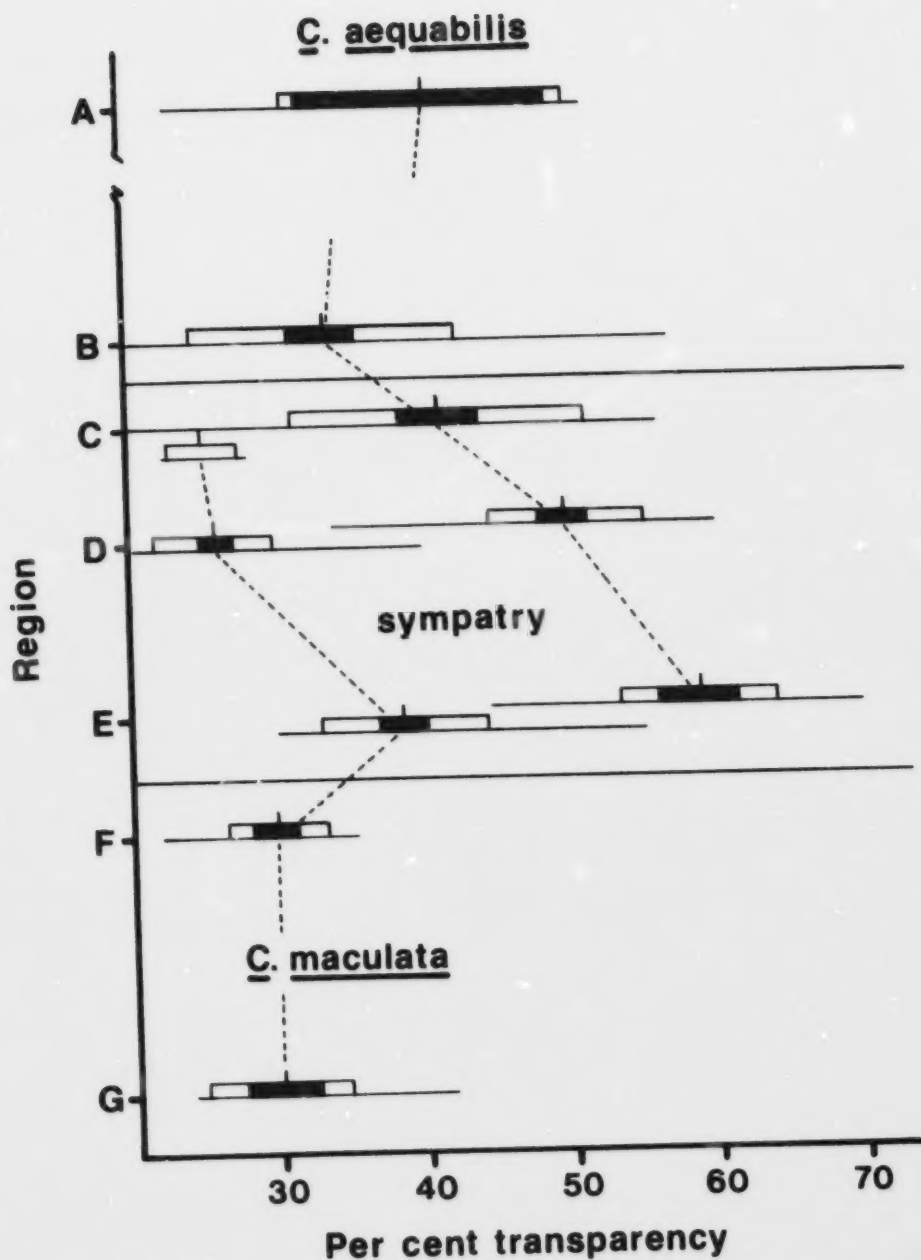


Fig. 8. Wing transparency in female damselflies (*Calopteryx aequabilis* and *C. maculata*) in sympatry and allopatry. Each sample is shown as a mean value, with black areas representing ± 1.96 standard errors, white areas ± 1 standard deviations, and the horizontal lines the range. (After Fig. 3 of Waage 1979.)

III. ETHOLOGICAL RESEARCH IN MUSEUMS

A. Traditional Collections

Traditional kinds of specimens and collections cannot be used in many research projects. There are several reasons for this: (a) it is often physically difficult or impossible to examine relevant characters because of a specimen's physical form or condition; (b) specimens are incomplete; and (c) sample sizes are often too small. I will discuss these points in turn (*a* and *b* together), and make suggestions for changes in our approach to specimen acquisition and preparation.

Morphological features that are important in social behaviour are often concealed or badly distorted in museum specimens. For example, wings of birds have many characteristics which reflect the extensive use of wings in displays, but wing feathers and surfaces cannot be adequately examined on standard museum round skins because wings are folded tightly against the flanks. Similarly, in small mammals, the topographic arrangement of lines, flashes, patterns, *etc.*, of mystacial vibrissae, and of skin glands, usually cannot be reliably judged using round skins. The structure of organs for signal emission or sensory reception can only be examined grossly in dried insects; and colours of fishes and many other taxa are often faded or lost altogether from specimens.

There are several general solutions to these and other problems. First, reasons for adhering to conventional specimen preparation should be examined. One of these reasons is that standardization facilitates communication, and allows researchers to exploit the resources of museums around the world. Yet in many cases a small departure from tradition can be made without compromising these values badly; it is possible to remove and spread one wing from each bird, for example, while retaining a nearly complete round skin. Related to this approach, institutions could diversify their methods of preparation while keeping part wholly conventional. Thus, a fraction of shrew skins could be treated in the field so that their skin glands are able to be studied histologically; some soft-bodied animals, or soft parts, can be freeze-dried to retain their shapes; and so on. There are many ways to treat specimens which are appropriate for specific research projects, but too specific for general museum collections, so procedures should be developed which allow for retention of the greatest amount of information, and for the greatest possible diversity of uses. In general, preparations which emphasize retention of more of each specimen, and more extensive notes and other documentation during preparation, will fulfill these goals best.

Many research questions discussed above (section II) demand adequate sample sizes and detailed information on specimens. It will become increasingly important to acquire samples encompassing socially significant variation due to such factors as age, social status, breeding status, circannual changes, *etc.* In consequence, the rationale for programmes of specimen acquisition and collection must be based increasingly upon gaps that exist in available collections — gaps because of inadequate sample sizes for various age groups, *etc.*, and for traditional specimens which carry too little intrinsic and extrinsic information. Many kinds of important information demand greater knowledge of individual animals before they are collected, a demand that is incompatible with much field collecting, and is certainly incompatible with traditional forms of field collecting. Thus a practical limit exists to the amount and kind of information which can be saved with specimens, except in specific research projects. Recognition of this limit forces us to ask whether much museum research should be concerned at all with behavioural questions which cannot be asked of the bulk of collections — even collections built around new standards of preparation and completeness (see section IV).

B. Associated Collections

1. Photographic and Cinematographic Collections

Still photography is useful for recording aspects of natural history which are relevant to social behaviour, including habitat, signs, sites of scent marking, nests, burrows, *etc.* (see section II.5 and Chapter 13). It is also useful for documenting those attributes of specimens which will be lost or distorted during preparation, including arrangement, shapes, and colour of soft parts. Still photography of behaviour provides valuable material for research, but usually in an auxiliary role to field studies, to provide more detailed and faithful records than are possible with an observer's descriptions.

The potential for systematic collecting and archiving of photographic material is largely unfulfilled. Some still-photographic collections in museums are used for placing significant occurrences on file, e.g. extralimital occurrences or aberrant specimens. One reason for the scarcity of collections more relevant to behaviour lies in the lack of clear purposes and procedures. Some guidelines for the development of photographic collections can come from the inadequacy of specimens for providing certain kinds of information, however. For example, museums which prepare birds as traditional study skins could establish procedures for routinely photographing both surfaces of a spread wing and the spread tail before preparations; such photographs could be valuable in many kinds of study on social morphology. Similarly, pigmentation patterns on the skin surfaces of odontocete whales are important in social communication and in systematics research; whales should be photographed in a standard fashion as soon after death as possible, to record these patterns (Evans and Bastian 1969; Mitchell 1970). It should be straightforward to provide protocols for systematically photographing unprepared specimens and features of their natural history. It is more difficult to envision organized collections of still photographs of behaviour, because most such material comes from specific studies by non-museum researchers, and is acquired for diverse purposes.

Cinematography is an invaluable component of research methodology in animal behaviour. It provides the most objective material documentation of behaviour, and has several major advantages over still photography: it can capture brief or unexpected events; it documents behaviour with a time base with fine resolution; and it is inherently freer from a photographer's bias than is still photography. The first two of these points are mentioned in guidelines for films added to the *Encyclopedia Cinematographica*, a scientific encyclopedia of 16 mm film:

"The kinds of phenomena recorded on film and included in the collection are those which have one or more of the following characteristics:

1. They cannot be observed by the unaided human eye and therefore demand the use of such film techniques as slow-motion or time-lapse cinematography.
2. They need to be compared with other phenomena — for which purpose verbal descriptions alone are inadequate.
3. They do not occur frequently; they are not readily available for observation by other scientists or students; or they are disappearing from the culture."

Cinematography is technically demanding and extremely expensive at all stages, from exposing film to storing and accessing it. These attributes make it unlikely that cinematographic collections will ever become common or even routine. By the same token, they also increase the value of existing collections. The world's largest scientific collection is *Encyclopedia Cinematographica*, in Göttingen, which includes many brief films (generally silent), each focussing on single phenomena or types of behaviour. The films are made as free from interpretation (including photographer bias) as possible, though most are accompanied by some written documentation. The nature of the films can be appreciated from their brevity and specificity (e.g. Laying of Scent Trail by Common Tree Shrew, *Tupaia glis*, 3 min; Damaging Fight in Shrimp, *Stenopus hispidus*, 6½ min; Displacement Eating during Frontal Threat in Butterfly Fish, *Chaetodon melanotus*, 3 min).

The *Encyclopedia Cinematographica* exemplifies a type of museum collection which is best centralized, in this case for technical and economic reasons. The collection consists of invaluable data records of behaviour, for this and future generations, and should be contributed to by all able researchers.

2. Audio Recordings

There are several compelling reasons for increasing the number and scope of audio recordings in collections, and for improving their documentation and quality. One reason is the demonstrated importance of animal sounds to an understanding of systematics, particularly at lower taxonomic levels, thus

¹Quoted from "Encyclopedia Cinematographica — A Unique Collection of Films in the Biological Sciences," Audio Visual Services, The Pennsylvania State University, University Park (not dated).

augmenting one of the most active research areas in museum zoology (e.g. Stein 1958, 1963; Thielcke 1964; Lanyon 1978; Johnson 1980; Booi 1982; Nikolski and Wallschläger 1982; Nussbaum *et al.* 1982). A second reason lies in our rapidly diminishing opportunities to study and record sounds of animals in relatively undisturbed social and ecological circumstances, and in the high extinction rates of many faunas (see section IV). Improved collections are relatively easily achieved, because sounds can now be captured with great fidelity by modern tape recording equipment.

Extant collections of audio recordings that are available and adequate for research purposes are widely dispersed among institutions and private individuals in many countries. The world's largest collections of bird sounds are held by the Library of Natural Sounds, Cornell University (approximately 45,000 recordings from approximately 4,500 species) and the Borror Laboratory of Bioacoustics, Ohio State University (approximately 18,000 recordings from approximately 800 species) (Boswall and Couzens 1982). Both of these institutional collections are dominated by bird sounds, a trend apparent in most collections. However, about 2,000 records of acoustic Orthoptera are held by the British Museum (Natural History), and amphibian sounds (particularly anuran) are well represented in some collections (Boswall and Kettle 1979). All other taxa are strongly under-represented (mammals, reptiles, fishes, arthropods other than insects, and other groups). The importance of audio recordings to current ornithological research can be illustrated by a recent summary by Gaunt (1983). He noted that 75% of the issues of a prominent ornithological journal included articles which dealt with sound analysis, from 1972 to 1981.

Despite the increasing use of acoustic analysis in zoological research, very few investigators deposit recordings in formal collections. Related to this, very few publications cross-refer to particular audio "specimens" in institutional collections, and many or most recordings in collections have inadequate behavioural documentation such as researchers could provide. I will deal with these points in turn.

It is conventional practice for series or individual specimens acquired in the course of research to be deposited in collections, where they are available to other researchers. Similarly, it is routine to refer to individual specimens or to the institutions where they are stored, or both, in systematic publications. The former is more difficult for audio recordings, because of the labour involved in editing and annotating tape recordings. However, it is impossible for interested investigators to re-examine material of interest if recordings are not placed in formal collections, so such a practice is highly desirable. Cross-reference to particular holdings would then become a matter of course, as it already is with a very small minority of workers (e.g. Lanyon 1978; Hardy and Wheat 1982).

A great many recordings are so poorly documented as to be almost valueless in ethological or systematic research. Often the only data available are species, date, and geographic location. Such information is often adequate for sounds which are readily homologized with other species or which are known from elsewhere, such as "primary song" of many male passerines. However, more detailed information is necessary in many instances, and always increases the value of recordings. For example, detailed documentation on social context is essential for those taxa with complex, highly graded vocal systems, or whose vocal expressions are closely linked to "emotional" state or subtle contextual variations (e.g. some insects, primates, ungulates, jacanas, phalaropes, guinea fowl; Howe 1972; Kiley 1972; Green 1975; Klingholz and Meynhardt 1979; Mace 1981; Harris *et al.* 1982; Maier 1982). In an attempt to improve and standardize the technical quality and documentation of recordings, the Library of Natural Sounds provides detailed data forms and instructions for recording, observing, and editing tapes, to recordists (Fig. 9). Similar protocols are not available at most smaller sound libraries, unfortunately, so many of their collections are far less valuable than they could be.

Sound libraries are similar to film libraries, in being relatively expensive and technically demanding to build and maintain. For these reasons, workers should contribute copies of their valuable recordings to one of the major collections, rather than building collections that are smaller, less valuable, less secure, and less accessible.

3. Other

Social behaviour of animals often alters the environment in specific ways. Such alterations include trails, runways, burrow systems, nests, scrapes, or scent marks. The majority of them can not be collected and archived as specimens, but merely described, measured, or photographed. Nevertheless, it is possible to establish collections of some artifacts, such as bird nests, the structure of which contains valuable information about ecogeographic variation or species-specific traits [e.g. weaver finches (Ploceidae) (Collias

and Collias 1964)]. Problems arise with the storage of many kinds of artifacts because they are large, or of a difficult shape to store, or are very fragile. Even so, selected examples could be acquired and augmented with extensive notes and photographs for other examples. The importance of field notes to such collections is apparent, a topic discussed further in Chapter 13.

IV. CONCLUDING REMARKS

Collections of specimens form the core of a research museum, and their care and study are prime responsibilities of museum scientists. What is the role of research on social behaviour in this context?

Knowledge of social behaviour and its evolutionary effects is enhanced by study of museum specimens. Feedback between field and museum studies can help establish criteria for improved and more complete specimen preparation, for the acquisition of associated information and material (notes, tapes, photographs, etc.), and for filling gaps in collections. Feedback can arise within research programs of individual scientists or departments, or can come from appraisal of developments and trends in ethology. In either case, museum scientists must integrate information about research that is often not centred on collections, or even concerned with them, in moulding curatorial and collecting policies and procedures. Consultation or collaboration with non-museum scientists is of obvious importance in this regard.

Many kinds of research (e.g. neurobiology) seem out of place in museums, because of their tenuous or remote links with information in specimens. In contrast, research of a comparative nature, or which takes place in the field, generally seems highly appropriate to museums, even though direct study of museum specimens may not always be involved. For example, information about behaviour or natural history is vital in much systematics research because of its sensitivity in pointing to affinities, especially at lower taxonomic levels. Some of this information can only come from dedicated research programs on behaviour with no reference to specimens, such as studies on rhythm variables as taxonomic characters in ants (McClusky and Soong 1979). Museum scientists are among the best qualified researchers to undertake studies of this sort, because of their strong training in systematic biology. Similarly, comprehensive natural-history studies on single or closely related species are naturally tied to field programs and to the field experience and training of museum scientists.

Major contributions to knowledge are likely to come from integrated field and museum research programs, often involving collaborators from different disciplines. Important areas of investigation include the relationships of trans-specific trends to adaptation at the population or species level, and of variation in morphological features to social behaviour. For example, why is intensity of advertisement calls strongly correlated with body size in male frogs intraspecifically but not interspecifically (Gerhardt 1975; Passmore 1981)? How do levels of intra- and interpopulational variation within species influence these patterns (e.g. Gerhardt and Mudry 1980; Gerhardt 1981)? Active collaboration, or simply the application of ideas from one realm in another, can significantly increase understanding. An example of the latter is the use of ideas about the importance of cephalic (and other) adornments in display behaviour, in interpreting the functions of antlers of the extinct Irish elk, and cranial structures in dinocephalians and hadrosaurs (Galton 1971; Gould 1974; Barghusen 1975; Hopson 1975). Interestingly, very little museum research on morphology or morphometrics of signalling structures in extant species has been sparked by behavioural observations (section II.A.5).

The collection, care, and study of specimens are serious undertakings in this time of massive and accelerating habitat destruction, and decimation or outright loss of many of the world's richest floras and faunas. Social behaviour is only one of many perspectives which can help shape our approaches to museum collecting and research in this context. The examples developed in this chapter support the view that naturalistic studies should precede or accompany collecting programs, that some specimens (at least) of each species should be prepared in unconventional ways, that specimens should include behaviourally significant variants, and that much information and material extrinsic to the specimens themselves should also be acquired and archived. For species which become extinct such materials will seem painfully sparse and inadequate, but they will be vastly richer than series of traditional preparations with collecting data tersely listed on labels.

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12. MUSEUM COLLECTIONS AND AQUATIC INVERTEBRATE ENVIRONMENTAL RESEARCH

R.O. Brinkhurst

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I. INTRODUCTION

The last two decades have seen a sudden increase in awareness of the environmental costs of human activities in nearly every sphere, coupled with the impact of population increase. While it has long been appreciated that man has rendered many species extinct and has damaged specific sites, many have come to recognize that the human species can and does produce regional and even global impacts by multiplying his own activities through technology. We begin to seek links between the abundance of dams on tributaries of the St. Lawrence River drainage, the pattern of run-off through the system, circulation on the continental shelf of Atlantic Canada, and productivity of one of the world's greatest fishery habitats, to cite but one example. Acid rain, and the build-up of atmospheric carbon dioxide, illustrate the hidden tax to be paid for the use of the atmosphere as a source of oxygen as a "fuel," and as a disposal site for gaseous wastes.

Our response to this increasing awareness has been to institutionalize our concern, and to seek controls to regulate our activities, in an attempt to harmonize them with our need for a viable ecosystem in which to operate as a biological species. National and regional governments have created or expanded agencies responsible for protecting air, water, and soil. The legislation developed by such agencies is continually resisted by those responsible for the development of wealth, employment, and development, and even by those traditionalists in departments concerned with the facilitation of exploitation in forestry, fisheries, and agriculture, who see environmental controls and the protection of ecological reserves as excessive. Whatever position one takes in the debate about the adequacy of environmental legislation and its implementation in various jurisdictions, one result of the change in our attitudes has been the requirement for ecological information on every sort of ecosystem all around the world. The whole paradigm of field biology has been forced to reflect the growing demand for information and prediction in support of ecological management decisions. Academic institutions have provided environmental studies programmes, institutes, or departments, though in some instances the staff maintain a primary allegiance to the classical departments. Methods for the detection and assessment of environmental damage have developed rapidly from the classical "indicator species" concept, to the "indicator association" approach, now made more objective and persuasive by the use of multivariate statistics such as those noted by Sundberg (1983).

All of these methods are fundamentally dependent on the basic data matrix of relative numbers of identified taxa at a series of sample sites. The provision of accurate and rapid identification of specimens from every possible ecosystem has become an urgent requirement of not only government and academic scientists, but also of the growing plethora of consultant agencies that have sprung up. For the first time outside the spheres of human and veterinary medicine and the control of agricultural and stored products pests, taxonomic guides, species lists, bibliographies and reference collections have become industrial tools.

For the museums, this new level of activity can be seen as either an opportunity or a danger, but either way administrators and curators must recognize that the world has changed permanently. Looked at from outside, the role of a museum taxonomist appears to consist of the curation and enhancement of the collection, contribution to the educational and interpretive functions of the museum for the public, and scientific research in a chosen sphere. Most museum biologists now combine an ecological interest

with the traditional taxonomic approach, and this has modified the older expedition concept into a perhaps sounder basis for the acquisition of material. The very basis of good taxonomy involves a meticulous attention to detail, and an accurate and verifiable creation of standard reference material. The resources available in terms of people, money, and storage space have rarely been adequate, especially for the less glamorous invertebrate groups. Consequently it is quite understandable if the sudden quantum increase in the number of people having to collect and identify aquatic invertebrates is seen to be a threat to the orderly development of museum science. The potential for erroneous identifications and range extensions by under-trained technicians working in industry and government, where there is considerable pressure to tackle very large surveys on very small budgets, is very real. While the large collections generated by such studies, often sited in remote and scientifically interesting localities (like the Beaufort Sea and Mackenzie River within our jurisdiction for example), are an invaluable source of new taxonomic and zoogeographic information, how can curators acquire such information and material, verify its accuracy, and not be completely overwhelmed by it?

II. BIOLOGY IN ENVIRONMENTAL ASSESSMENT

The concept of using living organisms to represent a synthesis of all of the abiotic and biotic factors of their ecosystems is far from novel. For example, the similarity in changes in plant associations with latitude or altitude are familiar to every schoolchild. The many attempts to classify lakes based on specific indicator species, largely a reflection of the oxygen regime and pH levels (reviewed by Brinkhurst 1974), were based on the same philosophy that certain species could be used to indicate a whole suite of limiting factors. Similarly, early attempts to document pollution levels in rivers made reference to the microbiota and eventually the macroinvertebrates. Both efforts can be traced to the beginning of the century, but they fell into disrepute with the advent of studies of process and function of ecosystems, with their basis in the concepts of productivity and energy flow, largely because of the lack of statistical methods to relate species abundances to localities. Experts could use data matrices as qualitative tools in the same way as the diagnostic physician may assess familiar symptoms in order to recognize disorders of the human body, but as the stakes were raised in the poker game between developers and environmentalists, and huge investments in terms of money and jobs became involved, the legal process required documented, quantitative, evidence. As engineers were traditionally charged with creating treatment processes for industry and municipalities, they came to control the detection and assessment process too. It is not surprising that such pragmatic people had difficulties accepting the evidence of expert witnesses, when it was based on visual inspection of data matrices in which one axis comprised a list of unpronounceable elongate Latin names! Data-reduction systems involving "point scores" and other circular arguments were rightly criticised by Hynes (1960) because too much information was lost in the process. The use of diversity indices represented the first step in rendering the data intelligible to non-biologists, but these indices suffer the fundamental flaw that, while hiding the strange Latin terminology from the engineers and laymen, the identities of the taxa are lost to the biologists too. Two environments can have the same diversity of fauna even if they have no species in common, which means the study reports based on such indices are still obliged to return to the expert interpretation of lists of names. While environmental stress certainly may tend to reduce diversity [though this has been challenged by Sundberg (1983)], the identity of the surviving species in a stressed ecosystem reveals the nature of that stress. In addition, natural shifts in substrate, for instance, will also lower diversity, and while it could be argued that field surveys should minimize the "noise" produced in data matrices created by sampling on a variety of substrates, real progress in this field was made when pollution biologists began using multivariate analyses. At last there were methods of data reduction available that could distinguish between samples with equivalent diversity composed of different taxa. Sadly, there are still many in the ranks of the pollution biologists who prefer, or are coerced, to limit their identifications to the crude separation of clams, midges, and worms, or who still cling to the diversity indices — having taken one step forward the second is refused! Admittedly, many of us are confused by the rich menu of methods available today, and are not capable of running the necessary analyses, but there is a whole generation of computer-literate young scientists emerging from the universities. However, no matter how sophisticated the data-reduction process, the original data base must be sound and is totally dependent upon good taxonomy.

III. PROVIDING THE TOOLS

The assessment of environmental impact now requires both field and laboratory scientific approaches coupled with legislative activity (Brinkhurst 1984). Laboratory toxicology is closely related to legislation by effluent regulation. In its strictest traditional sense the method relies on carefully reared and genetically controlled stocks of standard reference target species, such as rainbow trout. More recently, in an attempted compromise between the laboratory and field survey approaches, *in situ* flow-through bioassays have been developed, and these employ a diversity of species characteristic of the communities in the study site. It is imperative that the species used be identified accurately in order to make results obtained comparable with those in the literature, and this may often have to be done in conditions that are less than ideal. Information on the occurrence of test species in nearby localities can be helpful in making enough specimens available for testing.

While toxicological studies make some use of the kind of information provided by and based upon museum collections and their study (identity verification, sources of material), it is the field approach to detection and assessment that relies totally upon good taxonomy.

Despite the great difficulty encountered in applying the results of laboratory toxicology tests to predictions of ecological effects from effluent discharges, the field survey approach is still not generally accepted because of the slow appreciation of the recent objective quantification of the data obtained, as explained above. This situation should improve as the use of multivariate statistics spreads, but the lack of taxonomic expertise is still the weakest aspect of the work. Indeed, it is the cost associated with the process of identifying macroinvertebrate collections, from marine and freshwater aquatic ecosystems, which provides the main plank in the platform of those who would challenge the value of field studies. This cost could be drastically reduced if good, clear guides to taxonomic groups were more readily available. The need is for pragmatic, state-of-the-art, publications that can be produced cheaply and swiftly and can be periodically updated.

There is also a great deal of cynicism about the accuracy of many identifications made in the applied sphere. Non-biologists and administrators often fail to appreciate the necessity for obtaining accurate identifications of biological material, or the difficulty of them. Many taxonomic specialists are content to allow the process of classification and species description to progress at its traditional measured pace regardless of changed circumstances and are critical of any attempt to facilitate identification for non-experts. Again, positive steps to provide the needed tools would alleviate the problems of the ecologist, and would improve the quality of information that is of potential interest to the museum scientist.

The strange fact is that, even as the demand for assistance with identifications threatens to submerge those willing to supply the service, research managers, ever willing to seek out mandates in order to survive or even grow in times of diminishing budgets, still regard taxonomic work with a jaundiced eye. While the climate in science management is for practical science, the provision of the working tools for sophisticated ecological analysis still has an old-fashioned image.

The role of the museum in this activity should be examined with care. The ability of museums to respond appropriately depends upon what they, or their funding sources, see as their mandate. There is clearly a well known tug-of-war between the needs of display, public education, and entertainment, on the one hand, and of curation, preservation, and documentation, on the other. In the biological sciences any outsider can easily see the dominance of vertebrate collections and displays in Canada. This is partly due to the lay fixation with large animals, a term usually regarded as synonymous with mammals. Add to that the recognition of birds, common to the back yard of every citizen, and fish, familiar on the dinner table and from aquaria and recreational fishing, and the natural bias of our museums is revealed. Very few of our museums have any extensive staff to deal with the huge preponderance of invertebrates, which consist of at least 30 phyla in contrast to only one phylum for the vertebrates. The lack of technical assistance and space means that the invertebrate collections in many of our senior as well as smaller museums are not yet catalogued. Making these collections available and accessible to scientists, and carrying out their related interpretive mandates already stretches existing resources to breaking point in many instances. Despite this, our museum taxonomists often manage to pursue research on their own areas of specialization, contributing to the international pool of knowledge in the same way as do their academic and government colleagues.

The missing element that needs to be addressed is the responsibility for documenting the national fauna. It might be reasonable to say that academic and government scientists add teaching and manage-

ment or assessment responsibilities to their administrative and research duties, and so museum scientists might add the responsibility for documenting the national fauna in all groups to their curation and private research responsibilities, but it is clear that this is usually impossible with existing resources. In those sections dealing with invertebrates it is clearly impossible for any expansion of responsibility to be accommodated with existing low levels of support, even where the spirit is willing, and so perhaps the work may have to be undertaken by some new institutional arrangement.

In some political jurisdictions there once were clear mandates for providing regional surveys, but these groups (State Natural History Survey organizations in the United States for example) have often been coerced into diverting their attention increasingly towards ecology. Undoubtedly, an ecological background helps a systematist to keep some perspective in the taxonomic/zoogeographic work, but this cannot be done at the expense of the original mandate.

The need for pragmatic faunal guides is now gaining increased recognition. In Canada the recent efforts of the Entomological Society in conjunction with Supply and Services Canada have produced a first work of a series on Canadian insects (see McAlpine 1981). The Canadian Society of Zoologists is presently attempting to regenerate interest in a series of biological surveys of other faunal groups. Reinstatement of the short-lived Canadian Marine Fauna series of publications (see Berkeley and Berkeley 1948) would provide an outlet for a comprehensive series of taxonomic guides especially if an aggressive editor were to actively solicit contributions from the many active systematists across Canada. The mere existence of the Freshwater Biological Association faunal guides and the Linnaean Society guides in the United Kingdom, attracts contributions and periodic updates of the well documented British fauna. The scale of the equivalent effort required in Canada is, of course, very different in terms of geography and faunal diversity. The Pacific coast marine fauna is one of the most diverse anywhere, and the freshwater fauna is undoubtedly richer, region for region, than the depleted post-glacial insular fauna of Britain. The National Museum of Natural Sciences is attempting to construct a bibliography of Canadian invertebrates, and there are other local efforts. The British Columbia Provincial Museum produces handbooks to the local fauna. The Institute of Ocean Sciences generates or supports the production of species lists, bibliographies, and faunal guides (see Gardner and Szabo 1982) as well as maintaining world-wide studies on marine and freshwater oligochaetes. There is hope then, that there is a sufficient basis for and interest in this necessary work in Canada, but it is clear that it could be better focused and harnessed in view of the serious need, and that it is badly under supported. Less encouraging is the situation in regard to the collections of specimens and the attendant zoogeographic information generated by environmental studies.

IV. AN OPPORTUNITY

The explosive increase in the number and type of samples being collected by field biologists in connection with environmental monitoring and research is self-evident. Most of this material ends up being housed by organizations that cannot guarantee adequate storage, maintenance, accessibility, or even survival. Recent attempts by the Institute of Ocean Sciences, Pat Bay, to trace samples and data from the Beaufort Sea, now the target of exploration for fossil fuels, revealed that one consultant company had suffered a fire and lost all its archives, while another organization was no longer in existence. Companies charged with making a profit are surprisingly generous with storage space for samples, which they are required only occasionally to maintain by the terms of their contracts. As staff frequently cycle rapidly through such agencies, and staff costs are high, little real attempt can be made to curate collections for posterity. Government agencies, too, may hold old collections, but all too often they are stored in totally inadequate facilities or they suffer from periodic management reorganizations that may result in disposal of valuable material. Our museums are, at present, the only institutions with the basic core skills to take on the task of acquiring and maintaining collections, but they seem to be largely unable to respond to this new opportunity to profit by the collecting effort undertaken by others, even where they are aware of it. Many problems need to be overcome if this work is to be incorporated into our present museum systems. For example, the material may be bulky (the collection from my recent study of the benthos of one small part of the continental shelf of British Columbia filled several large packing cases). If it is to be the most use to the systematists this collection should be incorporated into the existing collections of the British Columbia Provincial Museum or the National Museums of Canada, where most of the material is now located. For ecologists and environmental work, however, it may be necessary to have the material

curated as a single collection. Such problems have been addressed, one example being the accession of the material collected by Mr. T. Beak into the collections of the Royal Ontario Museum. When searching for Canadian collections of aquatic oligochaetes I was able to derive much interesting material from this set of specimens. They were collected by Mr. Beak and the staff of his consulting company that pioneered industrial biological monitoring in Canada. Some years ago I was approached by one of the principals of the company that still bears Mr. Beak's name in regard to their interest in the proper disposition of a warehouse full of such collections, an invaluable resource for invertebrate studies in Canada. Apart from applauding the zeal of the company in maintaining the material, I could only deplore my inability to indicate a way in which the material could be exploited.

The Association of Systematic Collections has documented criteria for the selection of deposition sites for voucher specimens or collections, and has carefully reviewed many of the questions raised here (Lee 1978; Lee *et al.* 1982). Clearly, some selection process must be in place if we attempt to direct all collections of value to the museum shelves. As those authors indicate, there are no general statutes that require the proper disposition of voucher specimens or samples, though various government agencies in the United States are directed to deposit all collections of a wide variety of materials in the National Museum once a study has been completed. The enactors drafting this 1880 Act could not possibly foresee the flood tide that would be released today were it to be complied with rigorously. The Water Resources Board of California is one of the few agencies that can and does direct the acquisition and disposition of voucher specimens on a case-by-case basis. The State of Texas requires only vertebrates to be so deposited.

The National Oceans and Atmospheric Administration (United States Department of Commerce) maintains a National Oceanographic Data Center (N.O.D.C.), and this has extended its activities to the production of a list of computer codes for specific names as well as a (voluntary) form that they request accompany all data submissions to N.O.D.C. Such reporting of data and deposition of collections serve a dual purpose. There is an educational effect in alerting investigators to some of the wider implications of their work, even to suggesting that a clear purpose to each survey be identified. In addition, of course, the full value of the cost of collection and study is extracted if the taxa identified can be re-investigated as needed after subsequent taxonomic revision or deterioration of the collection site leading to repeated environmental assessment.

While the Information Services divisions of the Ocean Science and Surveys (Fisheries and Oceans Canada) are moving fast to accumulate data bases of previous scientific investigations for impact assessments, as yet there is no requirement written into the federal contracting-out policy requiring Supply and Services Canada to insert instructions into all appropriate contracts regarding the proper disposition of samples. While publications are properly documented and abstracted, the specimens upon which they depend are not necessarily deposited anywhere unless the work describes new taxa, in which case it is a fundamental taxonomic requirement.

Such a policy regarding deposition by provincial and federal government biologists would require some appropriate funding mechanism, some suggestions for which have been covered by Lee *et al.* (1982). The increasing activity in the museums should provide benefits to the general activity, by leading to improved basic support and an awareness of the significant part that systematists can play in the public and industrial domain. Better still might be the gradual expansion of "half-way" house systems such as identification centres in large institutions (as at the fisheries laboratory at St. Andrews, New Brunswick, which serves a federal agency, a cooperative educational institute, and the consultant industry), or state- or province-wide natural history surveys. In this way the new need for practical systematics and a high-volume operation may seem less of a challenge to the established values and historic mandates of existing systematic institutions. We need those who realise that conserving the future is as important as conserving the past, and we should begin to recognize the full implications of that idea in today's activities.

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13. MUSEUM COLLECTIONS AND LIFE-HISTORY STUDIES

G.A. Allen and R.A. Cannings

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I. INTRODUCTION

Studies of life histories have a long tradition as a part of natural history, and are an important part of modern ecology. Broadly speaking, life-history studies are concerned with all aspects of the life cycle of a species, particularly major events such as births and deaths and their frequency, timing and causes. Much of the older literature on life histories is descriptive. More recent work has focused on the evolution and ecology of life-history traits, and ultimately this may lead to predictions concerning the conditions under which particular life-history strategies evolve.

Life-history studies can be roughly divided into two broad areas: descriptive studies of the life cycle and the various life-history stages, and studies of life-table parameters such as age-specific fecundity and mortality. Information relevant to such studies includes not only reproductive behaviour and breeding system, but also such topics as the phenology of life stages, feeding habits, dormancy and migratory behaviour, territoriality, and competitive interactions between species. Key life-history traits include the nature and timing of reproductive effort, the relationship between reproduction and mortality, and intrapopulational variation in reproductive characteristics (Stearns 1976).

Natural history museums are committed to the long-term preservation of large and diverse collections representing a wide variety of taxa, for purposes of education and research. Museum research traditionally has emphasized studies of taxonomic and evolutionary relationships, and life-history features can be of great importance in such studies. However, museum collections are also logical places for life-history studies in themselves. The use of existing collections for such studies often makes possible the accumulation of large amounts of data in a short time, and reduces or eliminates the need for large investments of time and effort by individual researchers. Museum collections are rich sources of data for life-history studies, and are routinely used in this way for many groups of organisms. The kinds of information that can be extracted from collections depend on the nature of the collected material, the quality of the specimens and accompanying data, and the taxa under study.

Museum-based life-history studies in various taxonomic groups are considered in this chapter. The type of material available in museum collections, the kinds of information obtainable, and some example studies are discussed for each group. Data commonly available in collections are age, fecundity, and the phenology of major life-history events. In all taxa at least some inferences can be made about general life-history features from morphology, based on known relationships between structure and function established through studies of living systems (see Chapter 14). In some groups, large amounts of information may be obtained in this way.

II. LIFE-HISTORY INFORMATION FROM MUSEUM COLLECTIONS

A. Mammals

Mammals are preserved in museum collections as skulls, complete skeletons, study skins, or pelts. Fluid preservation is also useful, especially for small specimens, but has not been employed much except in specific tissue studies (Quay 1974), in food-habit studies in which stomach samples are preserved, or as a dumping ground for skinned carcasses or damaged specimens. Skins, skeletons, and whole specimens in fluid can provide various kinds of life-history information.

1. Age

Specimen ages may be used to estimate population age structures and to infer mortality schedules. In most mammals, external physical changes are visible which allow differentiation of juveniles from adults, but for many species more precise ageing methods exist. The bases for some of these follow:

a. Teeth The pattern of dentition changes markedly in many mammals during early life. The presence of deciduous or "milk" teeth and eruption patterns of permanent teeth can be used to assign relative ages to young animals. Such information is useful in the first two to five years of life, depending on the species, and has been obtained for various large mammals (Cowan 1936; Quimby and Gaab 1952; Brandborg 1955; Sows 1961; Hemming 1969; Frison and Reher 1970). For adult mammals, age can often be determined accurately from cementum lines deposited annually on tooth roots. This method has been employed with bears, using molars, premolars, or canines (Mundy and Fuller 1964; Willey 1974), and in various ungulates using incisors (Gilbert 1966; McCutchen 1969; Thomas and Bandy 1975; Turner 1977; Gasaway *et al.* 1978). Finally, patterns of tooth wear can be used to estimate relative age. This approach has been applied to the coyote (*Canis latrans*) (Gier 1957), and to several deer species (Peterson 1955; Robinette *et al.* 1957; Quimby and Gaab 1957).

b. Skeletal Development Two aspects of skeletal development, size and the loss of cartilage in long bones, are of some value in age estimation. Size is a somewhat unreliable predictor of age, since it may also be related to other factors such as nutritional status. Skull length and width are commonly used estimates of size, but other skeletal features such as closure of skull sutures, development of a sagittal crest, or length of long bones have also been used. Changes in the radius and ulna may be useful indicators of age in specimens of elk up to four years old (Knight 1966). Characteristic structures may develop at maturity in some species; one example is the lateral sesamoid tubercle on the femur of mink (*Mustela vison*) (Greer 1957).

Young animals can be aged by the degree of ossification of long bones: young Eastern Cottontails (*Sylvilagus floridanus*) in their first season show progressive loss of the epiphyseal cartilage of the humerus (Hale 1949); and young raccoons (*Procyon lotor*) show gradual closure of epiphyses in the radius and ulna (Sanderson 1961a). Methods like these are of little value for older specimens, however.

Males of some taxa (arctoid Carnivora, Chiroptera) have a baculum (penis bone) which changes in size and shape with age. This has been used to separate juvenile from adult males in many species (Friley 1949; Petrides 1950; Lechleitner 1954; Newby and Hawley 1954; Elder and Shanks 1962). According to Klevezal' and Kleinenberg (1967; cited in Larson and Taber 1980), layers similar to those in teeth are deposited in the periosteal layer of bones; the usefulness of this method for museum specimens is unknown, but it may be of value if the specimens have been appropriately preserved.

c. Horns and Antlers In mammals such as sheep and goats, age can be estimated (up to eight or ten years) from external growth ridges on the horns. These ridges may be related to fluctuations in nutrient availability or to growth checks during the breeding season; usually one ridge forms each winter (Larson and Taber 1980). In antlered species such as caribou (*Rangifer tarandus*), age may be estimated from bone-growth layers in the antler pedicels (Banfield 1960); this method is useful up to five years of age.

d. Eye Lenses The lens of the eye continues to increase in weight throughout life, and has been used to predict age in various mammals, including lagomorphs (Tiemeier and Plenert 1964) and carnivores (Sanderson 1961b; Mead 1967). The method can only be applied to whole museum specimens in which the lens is still present and has been preserved adequately. Age estimates tend to be less reliable in older specimens because of overlap between specimens of different age classes. A related technique is measurement of tyrosine levels in the eye lens; this has been used successfully with several species (Dapson and Irland 1972; Birney *et al.* 1975; Ludwig and Dapson 1977).

2. Fecundity

Fecundity information generally is not obtainable from skeletons or pelts but may be derived from preserved whole gravid females or from preserved reproductive structures. For example, placental scars can be used to estimate fecundity (Rolan and Gier 1967; Martin *et al.* 1976). In some mammals more indirect methods can be applied. For example, Cockburn *et al.* (1983) estimated litter size from nipple number in *Antechinus*, a small Australian marsupial. The relationship of body size (and by inference, age) to number of offspring and to fertility rate can be estimated from large series of whole specimens (Rolan and Gier 1967).

3. Phenology of Life-history Traits

Information on the timing of various life-history events such as courtship and mating periods, reproduction, and seasonal migrations may be obtained from well documented museum specimens. Birth dates may be determined from collection dates and ages of juvenile specimens. If intact specimens are available, the breeding season can often be judged from the condition of ovaries or testes, which show striking seasonal variation in many species (Jameson 1950; Larson and Taber 1980). Martin *et al.* (1976) summarize the usefulness of placental scar counts for indicating reproductive history in both monoestrous and polyestrous species of mammals.

Carriek and Ingham (1962) discuss the exceptional congruence between dentine layers in the teeth of the Southern Elephant Seal (*Mirounga leonina*) and the physiological and environmental conditions present during their deposition. These teeth are relatively easy to collect and preserve, and can provide detailed data on age, breeding activity and seasonal behaviour (see Figure 1).

4. Other Information

Series of bones or skins may reveal unusual features relevant to life histories of certain taxa. Howell and Hodgkin (1976) studied the microstructure of the hairs of glossophagine bats, which are obligate flower feeders during part of the year. Examination of the neck pelage on museum skins of 17 genera showed that the scales on the hairs angle sharply away from the shaft, trapping pollen grains which were later eaten by the bats during grooming. Pollen is nutritionally important to these bats, being the only reliable source of protein (Baker 1961).

Specimens preserved in fluid retain both internal and external parasites. Knowledge of host-parasite relationships may be important in the analysis of life histories, as parasites can have significant effects on growth rates, reproductive success, and morbidity or mortality of the host. Preparation of tissues for microscopic examination may reveal parasites not otherwise expected. For example, Quay (1974) examined a Narrow-skulled Pocket Mouse (*Perognathus artus*) which had been preserved whole in formalin, and found follicle mites in the sebaceous skin glands.

B. Birds

Birds are preserved in museum collections as skeletons, skins, or occasionally as whole specimens in formalin or alcohol; eggs and nests are also commonly collected. Various kinds of life-history information may be obtained from such collections, particularly information concerning fecundity.

1. Age

Plumage has a characteristic sequence of development in birds. Down (if present) is gradually replaced by juvenal and finally adult plumage. Foster (1967a) mapped the development of feather tracts in collections of nestling Orange-crowned Warblers (*Vermivora celata*) and used this information to estimate the age of specimens from plumage characteristics. The presence, colour, and extent of down, and the degree of development of adult plumage (especially development of primaries) has often been used in ageing the young of various ducks (Taber 1969) and gallinaceous birds (Chesness 1966). In gulls there are complex and variable changes in plumage with age. The breeding plumage may take two, three or four years to develop; in general, the smaller species start to breed at a younger age. Most species have a complete moult in the fall and a partial one in spring, thus plumages differ in summer and winter. The Ring-billed Gull (*Larus delawarensis*), which is typical of a three-year species, shows plumage changes with season as well as with increasing maturity of the individual (Grant 1982).

The colour of soft parts such as eyes and feet may also be useful in determining age. These parts are often not retained or suffer colour changes in dried museum specimens. However, supplementary material such as photographs and field notes can readily provide this information.

In most bird species there are no satisfactory methods of accurately ageing adult, sexually mature specimens. Degree of sexual maturity may be determined from the condition of ovaries or testes and from such features as the presence of the bursa of Fabricius (a small pouch opening off the cloaca in young birds); a large number of species also have characteristic plumage at sexual maturity, at least in certain seasons (Larson and Taber 1980).

2. Fecundity

Egg collections accompanied by good field data yield much useful information on fecundity in birds, since collections are normally made from a known full clutch. Clutch size, season, type of nest, and nesting locality can generally be determined. Since age of adult birds is usually unknown, age-specific fecundity data usually are not available. Many investigations of geographic variation in clutch size (fecundity) have been made using oological collections. Examples include work by Svensson (1978) on the Chaffinch (*Fringilla coelebs*), Murray (1976) on seven species of owls, Johnston (1954) on the Song Sparrow (*Melospiza melodia*), and Lack (1943) on the European Robin (*Erithacus rubecula*). Fecundity often increases with latitude, and may also increase toward the interior of a continent. Both of these are well known trends (Lack 1947; Cody 1966; Foster 1980; Ricklefs 1980a).

Bird skins can be examined to estimate the ratio of immature (first year) to adult birds in a species, giving an estimate of the recruitment or annual turnover rate. Ricklefs (1972) used this method in a study of the Rough-winged Swallow (*Stelgidopteryx ruficollis*). First-year birds were separated from adult males by the lack of serrations on the leading edge of the primary feathers. Ricklefs found the ratio of immatures to adults to be higher at higher latitudes, again suggesting an increase in fecundity with latitude.

Historical trends in fecundity can also be extracted from egg collections. This has been done in connection with studies of pesticide effects on life histories; for example, collections of eggs in areas of high organochlorine pesticide use can be compared with eggs taken from the same area in former years. Trends in fecundity and egg-shell thickness (correlated with hatching success) can then be analyzed (Anderson and Hickey 1972; Ohlendorf *et al.* 1978).

Some biases are inherent in data extracted from egg collections (Svensson 1978). Rarities and anomalies are favoured by egg collectors, and large clutches are preferred over small ones. In common species clutches in egg collections are mostly from the peak laying periods, since this is when fresh eggs are most easily obtained. Nest sites of difficult access or in remote localities are not examined as frequently as easily accessible ones. However, such difficulties are common to many kinds of field-related studies, and do not negate the value of the data obtained.

One problem with estimating fecundity from clutch size is the phenomenon of brood reduction through fratricide. In a number of bird species, older, larger nestlings may cause the death of younger, smaller siblings (Howe 1976; O'Connor 1978; Stinson 1979; Clark and Wilson 1981), either by killing them outright or by indirect harassment that prevents the subordinate nestling(s) from obtaining sufficient food or brooding (Edwards and Collopy 1983). Thus clutch sizes may be overestimates of the true produc-

tion of a nest. Data pertaining to brood reduction have been gathered from museum collections as well as from field studies. Fratricide is probable when size differences among siblings are great; this is common in eagle species with a clutch size of two. On the basis of studies of egg clutches in museums, Edwards and Collopy (1983) determined that eagle species with obligate fratricide show a longer hatching interval between eggs, with age differences between nestlings of up to four days. These authors also found within-clutch differences in egg volume of 12-13% for species with obligate fratricide, as compared with differences of 3-5% for those with facultative fratricide.

3. Phenology of Life-history Events

Well documented egg collections offer a wide range of phenological data, especially if associated with a nest-record-card system (see Fig. 2). Svensson (1978) used 612 clutches from Chaffinches (*Fringilla coelebs*) in Scandinavia to establish that the egg-laying period is four days earlier at present than it was in 1900. This change was correlated with a climatic shift that has produced earlier springs.

The breeding season of many species can be estimated from the presence of breeding plumage such as head plumes in cormorants and auklets or colourful bill sheaths in puffins. In whole preserved specimens the condition of the reproductive structures (eggs in oviduct, enlargement of testes) may also indicate breeding activity. Migration patterns, periods of flightlessness, and other life-history information may also be obtained from specimens or from locality information.

The relationship between plumage characteristics (indicators of sex and age) and migration has been studied using large numbers of museum specimens. Foster (1967b) analyzed the timing of plumage molts in four subspecies of Orange-crowned Warblers, and found differences in the prenuptial molt which were correlated with differences in spring migration times of sexes and subspecies. Johnson (1965) gathered information on the locality, date, sex, and age of spring migrant Hammond's Flycatchers (*Empidonax hammondi*) in western North America. He analyzed migration routes, the timing of migration in different regions, and the differential timing of migration by sex/age groups. In a similar study (Johnson 1970) he analyzed fall migration in the same species. Migrant birds of this species cannot be identified by sight in the field; museum collections are thus the only reliable source of information.

Adaptations of life-history parameters to environmental conditions have also been studied using museum collections. Holmes (1971) compared moult timing in populations of Dunlin or Red-backed Sandpipers (*Calidris alpina*) breeding in western Alaska (latitude 61°N) and northern Alaska (71°N). At the lower latitude, these sandpipers pair, nest, and care for the young before the onset of prebasic moult; thus breeding and moult do not overlap. At the higher latitude, breeding and moult overlap and the moult occurs faster, evidently owing to the constraints of a shorter and less predictable warm season.

The synchronization of host and parasite life cycles has sometimes been studied using avian museum specimens. Foster (1969) examined life cycles of the mallophagan lice *Ricinus picturatus* and *Menacanthus* sp. on the Orange-crowned Warbler, and found that the breeding time of the lice coincided with the nesting of the birds. This facilitated transfer of lice to newly hatched nestlings. Foster established the parasite-host relationship by locating unhatched louse eggs adhering to the plumage of museum specimens.

C. Reptiles and Amphibians

Specimens of these groups are generally preserved whole in alcohol. Museum collections may yield information on age distributions, reproduction, growth rates, and various other aspects of life history such as feeding habits and parasitism.

1. Age

In a number of reptiles, growth rings occur in vertebrae or long bones; these may represent annual periods of growth in temperate species such as the viper *Vipera aspis* (Castanet 1974). However, in many cases the relationship between age and number of rings has not been well established (Gibbons 1976), and there is evidence that bone growth-rings are unreliable indicators of age (Tinkle 1962; Suzuki 1963; Dobie 1971). Variation in number of rings may even occur between different bones within a specimen (Griffiths 1962).

BRITISH COLUMBIA NEST RECORDS SCHEME - B.C. Provincial Museum and B.C. Fish and Wildlife Branch, Victoria, B.C.

MAP GRID 82E/5	SPECIES SAY'S PHOEBE <i>Sayornis Sayi</i>	OBSERVERS NAME AND ADDRESS ROBERT A. CANNINGS B.C. PROVINCIAL MUSEUM VICTORIA, B.C. V8V 1X4	YEAR 1983
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Date (Write out month)	Eggs	Young	Comments, or Cowbird data	EXACT LOCATION
28 MARCH - 10 APRIL			BOTH SEXES BUILDING NEST	PENTICTON, B.C. WEST BENCH 705 SUNGLD DR.
16 APRIL	2	0	(10.00h) INCUBATION NOT STARTED	
17 APRIL	3	0	(10.10h) " " "	Altitude 1200 ft
19 APRIL	5	0	(11.20h) FEMALE ON NEST	NEST DESCRIPTION Ht. from ground 10 ft.
27 APRIL	5	0	(09.55h) " "	Material: FINE TWIGS, ROOTLETS, GRASSES AND FEATHERS FORMING A BULKY BOWL. SMALL AMOUNTS OF STRING USED, LINED WITH HORSEHAIR.
4 MAY	2	3	(10.15h) " "	Position: PLACED ON HORIZONTAL BEAM UNDER ROOF OF OPEN CARPORT
5 MAY	0	5	(10.10h) " "	Young with adults not found in nest
11 MAY	0	5	(11.25h) BOTH PARENTS FEEDING	Date ✓ No. Young ✓
18 MAY	0	5	(10.05h) " "	
23 MAY	0	→	(10.00h) ALL YOUNG LEFT	

ALSO FILL OUT BACK **NEST SUCCESSFULLY N**
AM.

☐ Mark X for COWBIRD USE, and fill out separate card for Cowbird.

CHECK THE BOX(ES) THAT DESCRIBE THE HABITAT

Special and Unique habitats	Open	✓
	Shrub	✓
	Forest	
	Grassland	
	Wetland	
	Coastal	
	Mountain	
	Other	
	Vegetation Types	✓
	Other	

Vegetation Structure	Open	✓
	Shrub	
	Forest	
	Grassland	
	Wetland	
	Coastal	
	Mountain	
	Other	
	Vegetation Types	✓
	Other	

Aquatic Systems	Open	✓
	Shrub	
	Forest	
	Grassland	
	Wetland	
	Coastal	
	Mountain	
	Other	
	Vegetation Types	✓
	Other	

COMMENTS:
(including predating effect of weather, etc.)

HABITAT: SMALL, WELL-TREED GARDEN BORDERED BY FRUIT ORCHARDS ON NORTH, EAST AND WEST. EXTENSIVE TRACT OF NATIVE GRASSLAND IMMEDIATELY TO THE SOUTH.

YOUNG REMAINED NEAR NEST AND ROOSTED ON SAME BEAM AT NIGHT UNTIL 23 JUNE.

FEMALE PRODUCED SECOND BROOD: FIRST EGG LAID 4 JUNE (SEE OTHER CARD)

No. Return completed cards by October 1 to: Mrs. L. A. Gibbard,
465 Ellis Street,
Penticton, B.C.
V2A 4M1

Fig. 2. An example of a completed nest-record card showing front (above) and back (below).

Certain species of turtles, for example the terrapin *Pseudemys scripta* (Cagle 1946; 1950), can be accurately aged from growth rings on the epidermal scutes of the shell. These rings result from alternating periods of rapid and slow shell growth, the slow growth rates being associated with winter hibernation in temperate species, although tropical species may show more than one ring per year (Gibbons 1976). This ageing method has been used successfully on some testudines (Legler 1960; Gaymer 1968; Gibbons 1968; Grubb 1971) but is not satisfactory for all species (Woodbury and Hardy 1948).

In many museum studies of reptiles, age is inferred from size, a technique which is workable for many snake species (Fitch 1965; Clark 1970; Gibbons 1972). The age-size relationship is less reliable for older individuals, however, even though size continues to increase during adult life (Gibbons 1976).

In amphibians, Schroeder and Baskett (1968) used annual growth marks on the posterior limb of the pterygoid bone to age bullfrogs (*Rana catesbeiana*) up to six years after metamorphosis. In the plethodontid salamander *Aneides lugubris*, osteological development has been used to estimate age (Wake *et al.* 1983); the long bones and pelvic plate continue to ossify throughout life, and the maxillary and dentary teeth decrease in number but increase in size and complexity. Senning (1940) aged *Necturus maculosus* using the parasphenoid bone while Organ (1961) used the number of lobes on each testis in *Desmognathus* salamanders. In extensive collections such as those of Organ (1961), Tilley (1973), and Daugherty and Sheldon (1982) discrete age classes are distinguishable. Metter (1967), studying tailed frog (*Ascaphus truei*) populations, found tadpole age classes could be separated using total length and the amount of limb development.

2. Fecundity and Reproductive Phenology

Information available from dissection of specimens includes clutch size, offspring size, sex ratio of offspring, duration of reproductive period, relationship between reproductive maturity and age (as inferred from size in most cases), and whether eggs or live young are produced. Timing of reproduction can be inferred from the size and development of ovaries or testes, the size and maturity of eggs (in females) and the presence of sperm in testes and vasa deferentia (in males). In the garter snake *Thamnophis sirtalis parietalis*, the number of young produced is related to the number of ovulation scars in the ovaries (Gregory 1977). Shine (1980a, b, 1981) has made extensive use of museum specimens to infer reproductive traits in several species of Australian elapid snakes (see Fig. 3).

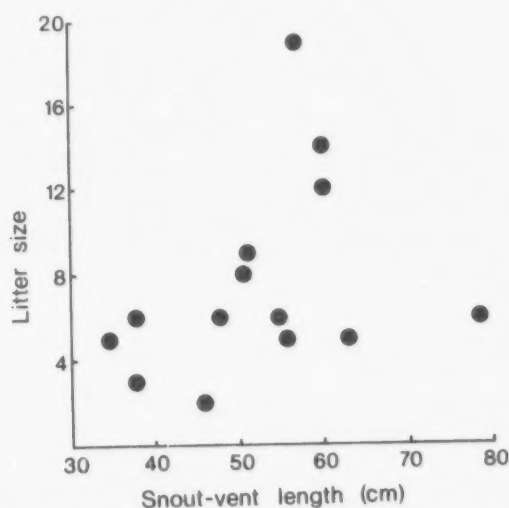


Fig. 3. Relationship of litter size to body size in females of the Death Adder, *Acanthophis antarcticus*, based on museum specimens. (From Fig. 4 of Shine 1980a.)

Using specimens of the microteiid lizard *Gymnophthalmus multiscutatus*, Vitt (1982) established the minimal size at sexual maturity, the clutch size and number of clutches, the mass of the eggs, and the period of reproduction. Punzo (1982) recorded data on clutch size and the production of multiple clutches (the latter based on the synchronous occurrence of yolking follicles and oviductal eggs or corpora lutea) in several species of desert lizards.

In a study of the tailed frog in Montana, Daugherty and Sheldon (1982) assigned adults of both sexes to cohorts based on total body length and (in females) reproductive condition. Reproductive males showed full development of black tubercles of the foreleg and chin, while the reproductive state of females was revealed by the condition of the egg mass. In females the ventral abdominal wall is transparent; the size of the egg mass and that of each individual egg can be measured. In addition, the colour of the fingertips is significant — white when the egg clutch is developing, black when it is completed. This study was based mainly on live material, but many of these details are also visible in preserved specimens. Metter (1967), studying the same species and using size-class data from specimens collected in different geographic areas in the Pacific Northwest, showed that all inland and three Cascade Mountain populations have a three-year larval period while populations along the coast and western Cascades have a larval period of two years.

Examining large collections (7,000 specimens of five species) of *Desmognathus* salamanders from Virginia, Organ (1961) developed some of the first comprehensive life tables for amphibians. Through the analysis of size-frequency information and other ageing methods, he determined population structure and survivorship curves for populations of several species. Organ discovered that the degree of terrestrial habit of these populations was related to length of the larval period, the proportion of individuals reaching sexual maturity, and the number of eggs produced per female.

Tilley (1973) studied preserved specimens of *Desmognathus ochrophaeus* from the Appalachian Mountains of North Carolina, and found that populations from different habitats differed from one another with respect to age at first reproduction. High-elevation populations matured later than those from low elevations, and woodland populations later than rock-dwelling ones. Delayed maturity was correlated with larger body size, greater fecundity, and higher survival in males.

3. Other Information

Examination of specimens and associated collection data may provide insight into life-history traits such as feeding habits (including variations in amount and in species eaten), growth rates, migratory habits, and periods of hibernation.

D. Fishes

Fishes are preserved in museum collections either as skeletons or as whole specimens in formalin or alcohol; specific structures such as otoliths may also be preserved separately. Life-history information such as age, fecundity, and the phenology of reproduction can be derived from such specimens, especially from fluid collections.

1. Age

Fishes of most species, particularly teleosts, may be aged by a variety of methods. Various hard tissues show regular fluctuations in the rate of deposition of material, leading to the formation of annual rings.

a. Scales Dermal scales in the skin of teleost fishes show concentric rings or circuli which are laid down in a regular pattern. A number of these are laid down in a year, and the circuli show variations in width that correlate with fluctuations in growth rate. Growth periods (as a result of variations in temperature, food availability, or other factors) commonly are annual, and the resulting annual variations in circuli can be used to age many temperate species (van Utrecht and Schenkkan 1972; Hofstede 1974). Annuli may be associated with low temperatures or with decreased food availability (Bilton 1974). Addi-

tional factors can sometimes influence growth rates of scales; many salmonids, for example, do not feed while migrating to spawning grounds, so their scales may also show growth checks due to spawning (Simkiss 1974). Such checks in growth vary from almost nonexistent for short migration distances, to quite marked for longer distances (Tautz and Land 1976). Age estimation using scales is not an infallible procedure, particularly in older specimens (Linfield 1974; Carlander 1974), but is a commonly used method adaptable to alcohol-preserved museum specimens.

b. Otoliths These calcareous structures are found in the statocysts (balancing organs) of teleosts, and show very regular annuli in many species due to the deposition of alternating hyaline and opaque layers of calcium carbonate (Pannella 1974, 1980). The sagittae, the largest otoliths present in each statocyst, are mainly used (Fig. 4). The rings in these structures often may be observed directly with reflected or transmitted light; sometimes the sagittae are sectioned or charred to make the rings more visible. Otoliths degenerate in formalin-preserved specimens but are well preserved in alcohol. They may also be removed from specimens at the time of collection and stored dry. Sagittae have been widely used in ageing of commercial fish species (Williams and Bedford 1974), and may also yield information on incidence of spawning, and within-year (daily or seasonal) fluctuations in growth (Pannella 1971, 1980).

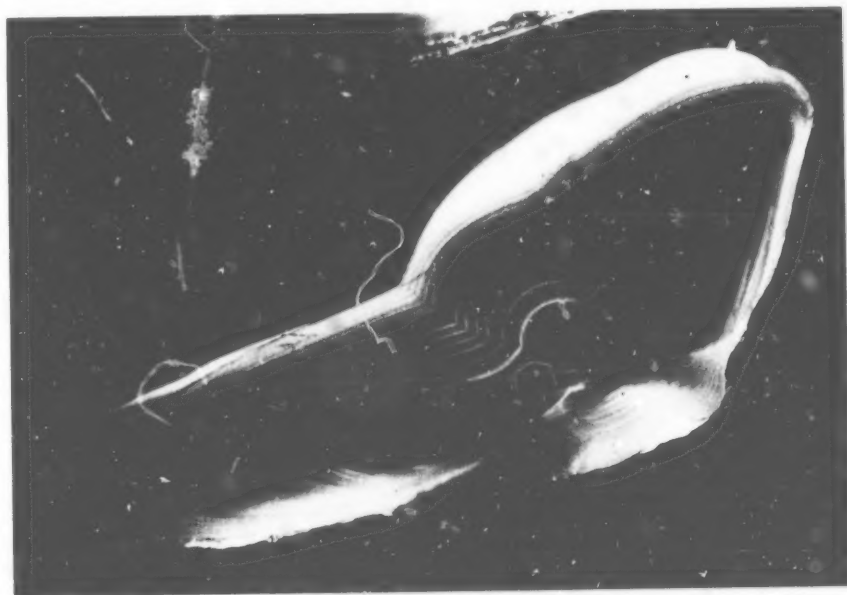


Fig. 4. An otolith of the Arctic Cod (*Gadus morhua*) as seen through the light microscope, showing 14 annual lines and five spawning zones. (From Plate 4 of Williams and Bedford 1974.)

c. Skeletal Structures Various parts of the skeleton may also show annuli corresponding to periods of growth.¹ Fin rays have been used in species such as bream (*Abramis brama*) (Deelder and Willemse 1973; Steinmetz 1974); age rings have also been found in the cleithrum, a flat bone in the pectoral girdle, in the pike *Esox lucius* (Casselman 1974), and in opercular bones of the ear in the tropical species *Tilapia melanotheron* (Fagade 1974).

¹Studies of calcium metabolism in fish (Simkiss 1974) have shown that there is rather active calcium exchange between hard and soft tissues, thus calcified structures may show deposition or resorption of calcium in response to various alterations in metabolism.

2. Fecundity

Estimates of fecundity may be made from numbers of eggs in gravid female specimens, and from numbers of larval stages present in samples of plankton. Good museum collections can provide a basis for various kinds of fecundity studies in fishes. For example, Stein (1980) found that abyssal species of liparids off the Pacific coast were less fecund than species found at shallow depths.

3. Phenology of Life-history Events

Timing of reproductive events in fishes may be estimated from collection dates of gravid females and larval stages. The ovaries and testes of adult fish show seasonal variation in their degree of development. O'Connell (1953), in a partly museum-based study of the Cabezon (*Scorpaenichthys marmoratus*), found that the reproductive structures of both males and females varied through several stages, from a "resting" or inactive state to spawning condition; the spawning season and sometimes the number of times an individual spawned in a season could be inferred from these stages. In some species, "spawning checks" in the scales or otoliths can be used to provide an indication of the years in which spawning occurs in individual fish (Williams and Bedford 1974; Tautz and Land 1976; Pannella 1980).

Stein (1980) studied preserved specimens of liparid fishes collected over 14 years from the continental slope and abyssal plain off Oregon. His study shows some of the information that can be gathered from systematic collections of populations that otherwise cannot be observed. He was able to compare reproduction in closely related species from different depths, and found that different species are either continuous or periodic breeders. He also collected information on egg size, fecundity (see above), and size at first reproduction. He concluded, from times of occurrence of ripe females and from the size distribution of ovarian eggs, that all species in the continuous spawning group were abyssal while at least some relatively shallow water species spawned seasonally.

Size-frequency distributions in large collections of a species may suggest protogynous hermaphroditism if male distributions are skewed compared to female ones (Cole 1983). Subsequent examination of gonad tissue can confirm such sex changes.

E. Molluscs

Museum collections may contain shells or whole specimens. Patterns of calcium carbonate deposition in the shell can yield information concerning the entire life history of individual animals.

1. Age

Many molluscs, particularly marine and freshwater bivalves, show diurnal or semidiurnal microgrowth increment patterns in the shell which are visible in cross sections under magnification (Lutz and Rhoads 1980). The width of these microgrowth increments varies seasonally as a result of environmental fluctuations (for example, temperature changes between summer and winter) or seasonal patterns of spawning. If the frequency and timing of these seasonal variations are known, the age of an individual can be determined with considerable precision (see Fig. 5). Temperate shallow-water species such as the subtidal cockle *Cerastoderma edule* show growth bands related to tidal fluctuations (Richardson *et al.* 1979), and may slow or cease growth when temperatures are low (Farrow 1971); deep-water species are generally subject to very little fluctuation in the environment, and major growth patterns are more commonly thought to indicate growth checks due to spawning (Rhoads and Pannella 1970).

2. Fecundity and Other Life-history Information

Shell growth patterns may be used in species inhabiting both constant and variable environments to determine timing and frequency of spawning events, age at death (and often season of death), and growth rates, including seasonal variation. In some cases major environmental events in the history of an individual specimen, such as sudden changes in temperature, storms, or unusually high or low tides, may also be observed. A detailed study of such microgrowth patterns in the eastern North American bivalve *Mercenaria mercenaria* was carried out by Kennish (1980).

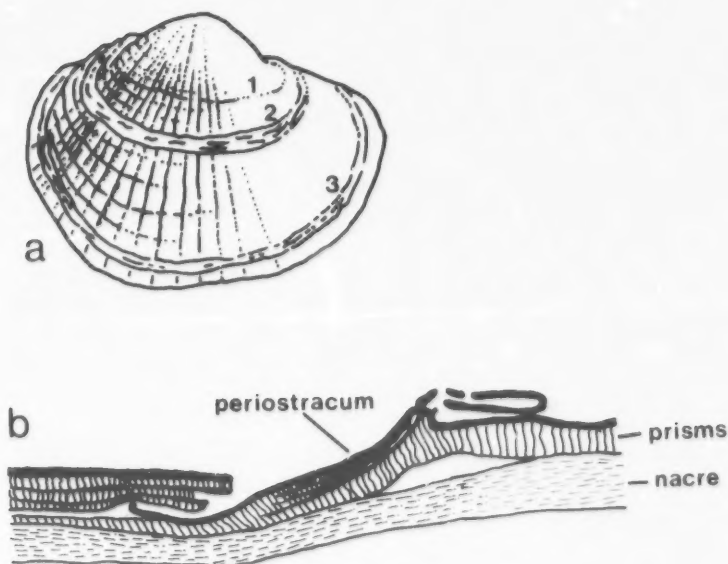


Fig. 5. a. Pseudoannual (1) and annual (2,3) growth bands on a bivalve shell. b. Transverse section of an annual growth band. (From Figs. 5 and 7 of Tevesz and Carter 1980.)

In series of whole specimens collected over several seasons, analysis of oocyte size-frequency distributions can give an indication of the reproductive chronology of some species. In the deep sea bivalve *Nuculana pontonia*, collections show that size distributions of oocytes are constant from season to season, indicating that reproduction occurs throughout the year (Rokop 1974).

F. Insects and Related Arthropods

Insects are preserved dried, in fluid (alcohol, glycerin, or fluid mixtures such as Kahle's solution), or on microscope slides. The diversity of these organisms necessitates a wide variety of preservation techniques (review by Martin 1977). Different stages of the same species are often preserved in different ways, and parts of dried or fluid-preserved specimens are frequently removed and stored separately for microscope examination. Insect products such as nests may also be collected. Many insects, particularly herbivores, have important interactions with particular food species; for these, specialized materials such as plant galls or food species showing characteristic feeding damage may be of special importance in life-history studies (Thompson 1916; Kinsey 1936).

1. Age

Insects and other terrestrial arthropods possess distinct life stages that can be used in ageing specimens. In both insects and arachnids the immature stages may be divided into several age/size classes (instars) representing the growth period between moults. Considerable morphological change may occur in the development of immatures, especially in arachnids and holometabolous insects. Adults do not grow and usually live only a short time, several hours to several months, although there are exceptions to this [uropygid arachnids may live to 14 years; mygalomorph spiders, 25 years (Savory 1977); queens of the ant

Lasius flavus, 22 years (Brian 1979); and reproductives of termites, up to 50 years (Imms 1957)]. Ageing adult specimens is not practicable in most groups. However, certain changes may occur in the adult integument which allow age determination in some species. The cuticle remains pale and weakly sclerotized up to a few days after emergence in many insects and these teneral specimens can easily be separated from older ones. Daily development of endocuticular layers may give estimates of adult age (Neville 1967); Veron (1973) found this approach useful in determining the post-teneral age of dragonflies. The development of pigment or pruinosity in adults is a measure of age (Parr 1973) although it does not necessarily proceed at a constant rate (Adetungi and Parr 1974). Johnson (1973) distinguished four post-teneral age groups in adults of the damselfly *Argia moesta* using colour change and increasing pruinosity on the thorax (Fig. 6). Jackson (1946) aged adult tsetse flies by wing wear, and fleas have been aged by the state of intactness of ctenidia and setae (Detinova 1968). In general, these techniques are limited to estimating relative ages, and in most cases they deal only with segments of the adult life span. Detailed age-estimation techniques can be established only through baseline field or cage studies, and more of such studies will greatly increase the value of museum specimens for life-history analyses.

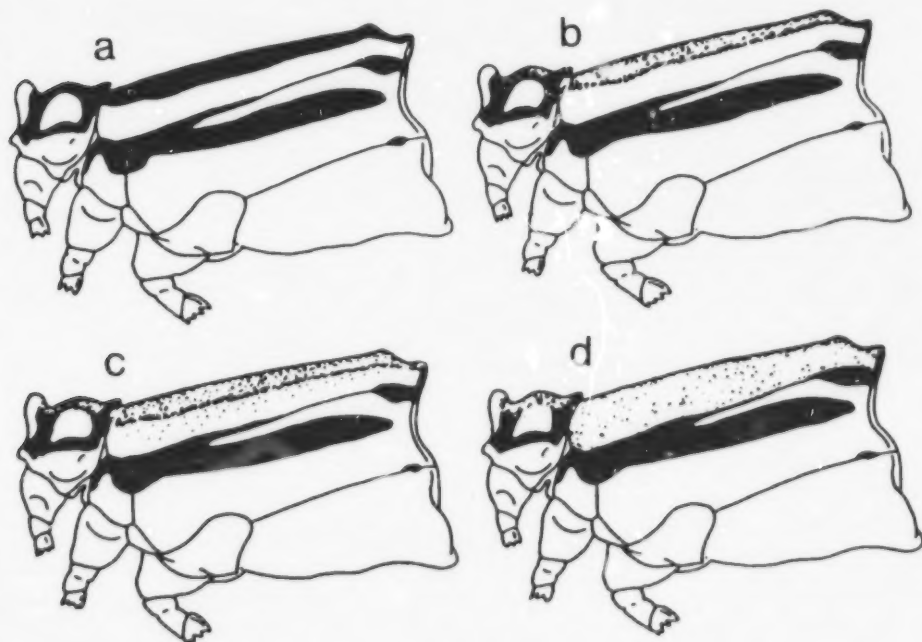


Fig. 6. Post-teneral stages in males of the dragonfly *Argia moesta* showing progressive development of thoracic pruinoscence (stippled). (From Fig. 4 of Johnson 1973.)

2. Fecundity

For insects, dried specimens are of little value in estimating fecundity. Johnson (1973) found that dissection of ovaries was possible in specimens preserved in 80% ethanol, but in his work on the damselfly *Argia moesta* he concluded that counts of ovarioles and eggs are too inaccurate to be reliable estimates of fecundity, at least in Odonata. Schmidt (1972), studying the more reduced reproductive system of the muscid fly *Hematobia irritans*, was able to count functional ovarioles but found no relationship to the known number of eggs laid. Many spiders, on the other hand, are collected with intact egg sacs and accurate counts of eggs can be made from alcohol collections.

3. Phenology of Life-history Traits and Other Information

The phenology of insect life stages and instars and the relationship of these stages to seasonal changes in population numbers can readily be examined in museum collections. Size-frequency distributions may supply information on life-cycle duration and recruitment rates of various larval instars. Evidence may also be gathered for the existence of complicated life histories, such as those of aphids where both sexually reproducing and parthenogenetic generations may occur, or those of social insects (Hymenoptera, Isoptera) where caste systems are found.

The timing of reproduction can be established from preserved specimens in many groups. In fluid-preserved Diptera certain changes in the ovaries have been used to estimate the number of ovipositions a female has made (Anderson 1964; Detinova 1968). This has been used mainly in medically important biting flies, some of which (such as mosquitoes) are not normally preserved in fluid. Mated tsetse fly females can be separated from unmated ones by the presence of "mating scars" on the abdominal sternites (Squire 1951). Dunkle (1979) used the mating marks on the eyes of female aeshnid dragon flies (left by the epiproct of the male during mating) for the same purpose. Older individuals showed deeper marks, indicating multiple matings; in addition, the large cerci of females of some genera normally break off during copulation. In the damselfly *Argia moesta* the grasp of the male's pruinose appendages leaves a pale spot on the female's prothorax that is visible in both dried and alcohol specimens. Although this spot indicates that tandem linkage has occurred, and not necessarily copulation, its presence is highly correlated with the existence of sperm in the spermatheca (visible even in dried specimens).

Collections can reveal variation in life histories caused by environmental gradients. Cannings *et al.* (1980) described differences in larval growth patterns, emergence times, and breeding and egg-laying periods in three *Lestes* damselflies occurring in lakes of varying salinity. Simple sequential collections yielded useful information on the life histories of the species, and also showed temporal separation of sympatric congeneric species owing to different development rates and local modification of phenology.

Migration and its role in life histories can be examined in insect collections. Collections of the migratory locust *Locusta migratoria* and a solitary grasshopper *L. danica* had long been confusing because of the existence of small numbers of intermediates. Finally it was discovered that these two "species" were forms of the same insect; the differences were caused mainly by environmental conditions, especially density (Williams 1958). It is known that each migratory locust species also has a solitary form; one phase can arise from the other with a shift in habitat conditions. Migrating locusts spread widely, but permanent breeding areas where solitary forms persist are more localized. Museum collections containing material of both phases can be used to locate outbreak sites and to track traditional migration patterns. These can be compared with climatological data for use in life-history research.

Other kinds of polymorphisms can be examined in a similar fashion. For example, polymorphic complexes may be revealed by pairs of mating specimens establishing mating between a male morph and two or more different female morphs. Such complexes are often mimetic, and geographical and phenological differences among morphs of a mimetic species can be related to the distributions and life histories of the models. A classic example is the butterfly *Papilio dardanus* of Africa; the male is monomorphic while the female has about 26 morphs, some of which mimic unrelated species (Sheppard 1961).

The presence of parasitism in preserved insects frequently can be recognized. Mermithid nematode parasitism enlarges the body and shortens the wings of blackflies (Strickland 1911) and causes malformation of the elytra in weevils (Poinar and Gyrisco 1962). These nematodes also cause "intersex" specimens with mixtures of male and female characters, especially reduction of the male genitalia, and shortening and thickening of the abdomen and antennae (Sublette 1964). Such parasites can have a significant impact on the life history of a species. Parasitized individuals are usually the last to pupate (Welch 1960) or to emerge (Nickle 1963). In many cases the host's activity is reduced (Welch 1965), and in chironomid midges parasitism can alter the mating swarm behaviour of males (Wulker 1961).

G. Other Invertebrates

1. Age

In many marine invertebrates growth is estimated using size-class data derived from multiple collections. Disk size, for example, is used to determine age in ophiuroids (Rokop 1974; Gage and Tyler 1982). Other indications of age may be used in some groups. Annual growth lines have been found in the jaws of

a number of benthic phyllodoce morph polychaete worms (Kirkegaard 1970; Olive 1980), and apparently are related to reproduction. Annual rings related to fluctuations in water temperature can be seen in the calcareous skeletons of scleractinid corals (Dodge and Vaišnys 1980).

2. Fecundity and Reproduction

The size structure of populations can help determine reproductive chronology. If size-frequency distributions are similar throughout the year, as in the ophiuroid *Ophiomusium lymani*, year-round recruitment and continuous reproduction can be inferred (Rokop 1974). In some groups, oocyte size-frequency distributions can also give this information; Rokop used this method to show that the brachiopod *Frieleia halli* and the scaphopod *Cadulus californicus* had seasonal breeding cycles in the San Diego trough. In addition, counts of oocytes provided estimates of fecundity.

H. Vascular Plants

Museum specimens of vascular plants are usually preserved dry, pressed flat, and mounted on light cardboard. Depending on their size, specimens may be whole plants or representative portions with reproductive structures. Selected tissues such as delicate flowers or fruits may be preserved in alcohol-formalin fixative. More specialized materials are collected for some groups of plants (for example, wood samples from woody species). The value of a specimen is enhanced greatly by detailed collection information.

1. Age

In most herbaceous plant species it is not possible to estimate age, but there are some exceptions. In perennial rhizomatous species, age may be correlated with extent of rhizome, as in the Bracken Fern (*Pteridium aquilinum*) (Oinonen 1967), but in many such species the individuals are too large for an entire plant to be collected. Some species exhibit rhizome scars indicating annual growth increments or the annual development of above-ground shoots (Silvertown 1982). The Blazing-star (*Liatris aspera*) can be accurately aged from growth rings in the corms (Kerster 1968). The bulb of the Trout Lily (*Erythronium americanum*) produces a new outer layer each year, and the layers or sheafs of previous years remain attached; in carefully preserved specimens the age can be determined up to about 15 years (Holland 1981). All of these methods may suffer from the problem that beyond a certain age the old tissues decay and disappear, so ages may actually be minimal estimates.

Woody species can often be aged with a high degree of success. Shrubs, with multiple stems of different ages, may be difficult to age precisely, since an entire plant may be considerably older than the individual stems present (Harper 1977); sometimes, however, the rhizomes can be aged, as in the Snowberry (*Symphoricarpos occidentalis*) (Pelton 1953). Single-stemmed woody species may be aged from cores taken through the centre (pith) of the stem near ground level (Oosting and Billings 1951; Roughton 1962). Temperate woody plant species deposit annual rings of xylem with great regularity, and information about growth rates as well as age can be obtained (Fig. 7). Inferences can also be made about climate and about periodic disturbances such as fire. There are some difficulties with age determination from tree rings. Woody species may occasionally form more than one ring in a year, as the result of growth interruptions due to adverse conditions during the growing season (Barrow *et al.* 1968). In old specimens, counts of rings from earliest years are sometimes difficult to obtain, especially if decay of the heartwood has occurred. Finally, tropical tree species generally do not form annual rings, so the method is mainly of use in temperate species.

2. Fecundity

When an entire individual has been collected, potential and sometimes actual fecundity may be estimated from the number of flowers or fruits (or other reproductive structures); dissection of ovaries to determine ovule or seed number is often possible. In some families of flowering plants, fully developed

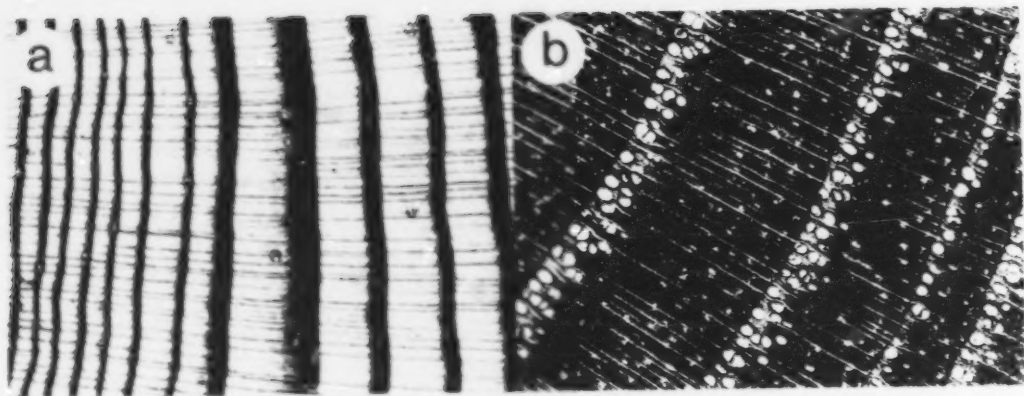


Fig. 7. Annual growth rings in xylem of trees, showing year-to-year variation in growth. a, Tamarack (*Larix laricina*); b, White Ash (*Fraxinus americana*).

fruits are required for proper identification and are thus routinely collected, and fecundity estimates can often be made quite accurately. Even when seeds have been shed, their number often can be determined from markings or scars in the mature ovary, or (in taxa with a known and constant number of seeds per fruit) from scars left by fruiting structures on the plant. A case in point is a Century Plant (*Agave palmeri*), in which the number of viable seeds produced can be determined from dark markings left on the inner surfaces of the seed capsules. Howell and Roth (1981) made use of this feature in a study of plant-pollinator interactions between *A. palmeri* and the bat *Leptonycteris sanborni*; by examining capsules on herbarium specimens, they were able to document a gradual decline in seed set (correlated with a corresponding decline in bat populations) over a period of 40 years.

For large species, only rough estimates of fecundity are possible since the reproductive structures on museum specimens may represent only a small part of the reproductive output, and reproductive structures are not always distributed uniformly on the plant.

3. Phenology of Life-history Events

Herbarium specimens are of great value in estimating flowering and fruiting dates and their variation between years and localities. It is sometimes possible to relate these variations to site features such as moisture availability, elevation, or latitude. Other life-history features such as periods of dormancy may also be determined, although dormant stages are found less commonly in museum collections.

1. Non-vascular Plants

These are preserved as dried specimens or in alcohol. Many algae are hygroscopic and are treated with formaldehyde before drying. Life-history information obtainable from specimens of these groups (bryophytes, lichens, algae, fungi) is limited. Very rough fecundity estimates may be obtained. The phenology of various reproductive states (sporophyte development in bryophytes, sporophyte and gametophyte reproductive stages of algae) can be estimated quite accurately. Fruiting structures of fungi are routinely collected and may be preserved wet or dry. The life histories of most fungi have not been well studied, and in some cases the various life stages and the mode of reproduction are virtually unknown. Fungi of many species do have one advantage: dried fruiting structures often yield spores from which live cultures can be established.

III. IMPROVING THE USEFULNESS OF MUSEUM COLLECTIONS

Considerable information on life histories can be extracted from museum collections as they presently exist, but the value of these collections for life-history studies could be enhanced in various ways with relatively little effort.

A. Completeness of Collections

If there is one theme to be stressed here, it is the need for better and more complete collecting. In some disciplines the rate of museum collecting has declined significantly over the past few decades as local biotas have become better known. In ornithology, for example, museum-based systematic work has declined in favour of theoretical or field-oriented research (Ricklefs 1980b; Olson 1981). Ricklefs has urged the use of museum collections for ecological research, especially "morphological approaches to annual cycles" and other kinds of life-history studies. "Museum ecology," as Ricklefs (1980b) calls it, exploits the huge volume of information available in museum collections. The broadening of museum collections to include more ecologically valuable material will also strengthen the museum community's ties with other biologists and sources of funding, a prerequisite to attracting and training a new generation of museum researchers (Ricklefs 1981).

The increasing rate of habitat destruction in all parts of the world makes collecting in vulnerable areas of vital importance to our understanding of the diversity of life. This is particularly crucial in parts of the tropics, but is also of great importance in temperate regions. For example, in Canada, a country with a relatively well understood biota and an active scientific community, half the estimated 60,000 insect species remain undescribed (Danks 1979). Even for those species which are taxonomically well understood, collections necessary for the most basic life-history information are often lacking. In the Canadian insect fauna only 1,016 of 7,058 known species of Diptera, 933 of 6,748 Coleoptera, and 20 of 354 species of oribatid mites have any immature stages described (Danks 1979).

A drawback to many museum collections is that they contain relatively few examples of any one species. In order to estimate life-history events accurately, large numbers of specimens (representing different age and sex groups, seasons of collection, and localities) must be examined. Of particular value are repeated collections of a species from the same locality or population. If collection intervals are short, this may allow detailed determination of phenology of life-history stages, as in insects. Over a longer period, sufficient information may be gathered from collections to assess rates of mortality and fecundity. These rates often fluctuate, and repeated samples from the same populations allow these fluctuations to be documented.

B. Label Data and Accessory Information

The utility of a specimen in many instances is a direct function of the detail and accuracy of label information. This information allows the phenology of basic life history parameters to be determined, and makes possible the establishment of correlations between life-history features and environment. Unusual life-history features may also be revealed from label information; the dates associated with colour morphs of the European nymphalid butterfly *Araschnia levana* gave the first indication that these were different generations of the same species (Beck 1968).

Examples of the kinds of data that should be collected (and either attached to the specimen or cross-referenced with it) are given in Martin (1977) and Nagorsen and Peterson (1980). Field notes amplify the label data tremendously and add information that at the time of writing may not be considered important, but which during later studies may be of great value. Collectors should keep detailed field notes; these documents can be accessioned along with the specimen material as part of a museum's collection.

Photograph collections may be invaluable complements to collection documentation (Lambert *et al.* 1983). Photographs relate life-history information to the environment accurately and concisely, and are one of the best ways of documenting habitat, breeding sites, and behaviour. Colour photographs of live or freshly caught specimens may help identify or age them, as key characteristics sometimes disappear or become modified with death and preservation (see Chapter 11).

C. Variety and Consistency of Collecting Methods

A variety of collecting methods must often be used in order to collect adequately all life stages of a species. Thus a particular toad may be picked up from under a log, but its larva will have to be netted from a nearby pond. An adult bot fly may be caught in a malaise trap or hand net, but its larva may be found only in the body of a trapped mouse. Consistency in collection (as in methods of preserving) is also important. Collections of particular life stages of a species should be made in a standardized manner if different specimens are to be comparable.

Different preservation methods allow the extraction of different kinds of life-history information from a specimen, and since no one method provides material suitable for all kinds of studies, a variety of methods should be used. For example, birds or mammals may be preserved as skins, skeletons, or whole specimens in fluid; selected organs or tissue samples (blood samples, skin with ectoparasites, eye lenses, digestive system for dietary analysis) may be removed and preserved separately. Simple modifications of standard methods, such as detaching and spreading one wing of a bird skin so that age-specific plumage features are visible, are often valuable. A useful general method for birds and mammals is to fix and preserve whole specimens of a taxon in fluid (Quay 1974); these can then be processed further in various ways. The methods adopted for a particular group should be those that maintain the usefulness of the specimen for the widest range of studies.

The need for more fluid collections of birds and mammals is being recognized by more and more researchers, and to increase the efficiency of collection management and research planning, the Committee on Collections of the American Ornithologists Union is preparing inventories of avian anatomical collections worldwide (Zusi *et al.* 1982). Only one-third of the world's bird species are available in fluid and skeleton collections. A similar difficulty exists with plant collections. Pressed specimens of vascular plants yield much valuable information, but fluid collections are more suitable for preserving delicate three-dimensional morphological structures or internal anatomical features.

D. Specialized Collections for Specific Purposes

1. Nest-record Schemes

Nest-record-card programs are a valuable supplement to ornithological collections. These programs are a good example of data banks that permit the extraction of significant life-history parameters. The basis of such a scheme is a printed card that is filled in by an ornithologist or interested naturalist when a nest is found and observed for any length of time (Fig. 2). Completed cards are then sorted and filed in a central location; the computerization of the scheme adds greatly to its usefulness. Nest-record schemes housed in museums can be cross-referenced to the oological collections when cards refer to clutches or nestlings collected subsequently. This is the procedure in the Nest Record Scheme begun in 1955 and housed in the British Columbia Provincial Museum.

These programs provide valuable data on the growth of young as well as on eggs. The large numbers of records available can contribute greatly to the statistical strength of ornithological studies; for example, no single researcher could obtain the breadth of data that Peakall (1970) took from 8,108 nest-record cards in his study of reproduction in the Eastern Bluebird. Nest-record schemes are much used in studies of breeding birds. The initial program, begun under the auspices of the British Trust for Ornithology in 1939, contained 238,000 cards by 1970 (Peakall 1970), and many of the most significant life-history studies of British birds have depended on its data (Burton and Mayer-Gross 1965). The more visits are made to the nest, and the more fully and accurately the card is filled in, the better and more useful are the data obtained. Completed cards must be screened by competent workers since the field experience of those submitting cards is often variable. Life-history information from cards may include clutch-initiation date, laying interval, clutch size, incubation period, hatching dates, hatching success, nesting period, fledging dates, fledging success, predation, parasitism, and descriptions of feeding, nest construction and nest site.

2. Collections From Environmental Impact Studies

Large collections are often made in the course of environmental impact or environmental monitoring studies (see Chapter 12). After such projects are completed the specimens are often discarded, or only synoptic collections are retained. The lack of detailed collections of taxa over time at a single location is a major drawback of museum collections with respect to life-history studies, and the preservation of such material should be strongly encouraged.

3. Material Documenting Species Interactions

Many species have specific ecological relationships (such as parasite-host or predator-prey) with other taxa, and important information about such relationships can be gathered from properly collected and documented specimens. Mulvey and Anderson (1980), in describing a new species of root-knot nematode (*Meloidogyne sewellii*), gave cross-referenced collection data for the nematode and its spike-rush host.

A particular predator, parasite, or pathogen may cause characteristic damage to host tissues. The damaged material should be preserved, since it can be of considerable value in obtaining such information as geographic range, host preferences or phenology of events in the predator's life cycle (Condon and Whalen 1983). In gall-forming Diptera and Hymenoptera, the gall may be of importance in determining fecundity (Weis *et al.* 1983) as well as for identification. Condon and Whalen (1983) pointed out that herbivore- and pathogen-damaged plant materials are specifically avoided by collectors, and suggested that special collections of such materials should be maintained by at least some of the major herbaria.

4. Specimens from Rearing Studies

The association of life stages is vital in life-history research. Material derived from rearings of organisms should be deposited in museum collections where the information it contains can be put to use. Rearings are the main method, for example, of determining the life stages of insects or the seedling and juvenile stages of plants; information on growth rates may also be a by-product of such studies.

E. The Relationship Between Museum Collections and Living Systems

Museum collections are of maximal usefulness when the data they make available are interpreted in the light of studies of living systems. In the absence of such studies, collections are often under-utilized. In many species, life-history information is inferred from the relationship between a variable that can be measured on a museum specimen (such as size), and some actual life-history parameter (for example, age). Most methods for ageing organisms have been verified by examination of many specimens of known age. Thus, the study of live organisms increases the usefulness of museum collections; and collections in turn extend our knowledge of life histories much further than would otherwise be possible, by extending the number and variety of specimens serving as a data base. This interaction could be further extended by the establishment of one-to-one correspondence between individual live and preserved specimens — an approach possible in some large and long-lived species of indeterminate growth form, such as trees.

Ultimately the effort invested in collecting and preserving museum specimens must be justified by their potential contributions to scientific knowledge. Many kinds of life-history information can only be obtained from living populations, or require corroboration from living material to establish their significance. Ecologists studying life histories usually make their own collections to obtain answers to specific questions. Nevertheless general museum collections can be adapted and improved to yield large amounts of information for many kinds of life-history studies, and imaginative and innovative approaches are needed both in collecting methods and in research if museum collections are to realize their potential value in this field.

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14. THE ROLE OF SCIENTIFIC COLLECTIONS IN ECOLOGICAL MORPHOLOGY

John W. Fitzpatrick

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I. INTRODUCTION

Ecology is a relative newcomer to the biological sciences, for one good and simple reason: until recently, biologists intrigued by the organismic world were still busy collecting, cataloguing, naming, and inventorying that world. Few features of a gigantic puzzle can be recognized until one finds and recognizes a reasonable fraction of its pieces. The biotic world is an enormous puzzle indeed, and the pieces that make it up are biological populations and species. Over the past two centuries, small but representative samples of these pieces have been collected, named, and made available for description, scrutiny, dissection, measurement, comparison, and organization. These samples — scientific specimens — are safeguarded and studied within the vast natural libraries we call museums, institutions with a well-established central role in solving the enormous puzzle bit by bit.

II. ECOLOGY AND THE MUSEUM

Principally through the growth and analysis of scientific collections, systematists by the 1980s have named a substantial proportion of the world's *species*, and have been able to turn increasingly toward the job of unravelling the evolutionary history that connects them. Armed with the species' names (many now available in field guide format), ecologists, in turn, have all but completed their own cataloguing of *species assemblages* around the world. From this exercise they have been able to turn increasingly toward analyzing the dynamics of *species interactions*, unravelling the structure and function of whole communities. It is clear to anyone who has personally dabbled across this progression of disciplines that each step can be only as strong as the preceding discipline upon which it is founded. Ecology, even at its most theoretical levels, is useful only to the extent that it sheds light on real interactions within real communities of properly identified populations, and in the context of historical constraints on those populations. Hence, an ecologist either must have faith in his partners in museums or, better yet, must visit those museums occasionally himself (incidentally, thereby providing real-world insights to some museum systematists who never study their organisms in the wild).

Along these lines, a recent emotional exchange of views on the museum tradition in ornithology by a "pure" ecologist and a "pure" systematist (Ricklefs 1980; Olson 1981) would represent a fine parody of scientific parochialism were its implications not more serious. The disciplines of ecology and systematics are one, inseparable and interdependent. Yet, their practitioners seem unusually prone to lose sight of the fact that many of the finest modern ecologists have roots in systematics, and that the very best systematists are those who incorporate data on the living organism into their analyses.

Central to the present essay are two premises: (1) we cannot adequately classify species or effectively study their evolutionary modifications and relationships without careful attention to the environmental settings in which they live day by day and generation by generation; equally, (2) we cannot fully understand the nature and effects of species interactions in a community without attention to the evolutionary history of those species, their phylogenetic affinities, and the constraints that structure itself places upon behaviour and adaptation. All of these broad aspects of evolutionary biology depend upon carefully assembled scientific collections, as integral resources for data, comparative analysis, and verification.

III. ECOLOGICAL MORPHOLOGY

Ecology constitutes a search for patterns in a world full of highly complicated and variable biological interactions. Through logical interpretations, inferences, and deductions we attempt to generalize these patterns and make predictions from them, with which we test and modify our hypotheses. However, a peculiar feature of ecology separates it from many other branches of science, including much of biology. In biochemistry, cellular biology, molecular biology, and genetics, for example, many important unsolved problems are relatively easy to identify, conceptualize, and describe. Physical techniques for solving these problems often pose the most serious limitations to progress in such fields. These areas of biology advance as much from technical breakthroughs and their implications as they do from new concepts. In ecology, by contrast, the most elusive and difficult hurdles lie in conceiving the interesting classes of problems to address, followed by correctly posing the scientific question. Once these are accomplished, the physical techniques usually boil down to careful observations, estimations, and measurements followed by statistical treatment of the data. Although frequently tedious, and occasionally strenuous, these jobs are relatively easy to design and execute *once the question is properly formulated*.

Morphology — the study of the size and shape of organisms — is another example of a discipline in which scientific progress is dependent more upon the nature and precision of the question than on the technical process of answering it. "Ecological morphology" describes the realm of questions about body sizes and shapes that relate directly to the community interactions in which the bodies participate. Broadly speaking, this realm includes aspects of genetics, growth and development, physiology, and especially functional anatomy. However, as these areas are discussed elsewhere in this volume, and most are outside my own expertise, I shall simply nod to them here, acknowledging that they do directly influence the ecological implications of body shape, and that they too depend upon scientific collections for their raw materials.

My musings henceforth are concerned with the *external* size, shape, and structure of organisms. My goals are to outline some questions about the interactions between body form and environment, and to pose them in ways that illuminate the kinds of measurements needed to answer them. Although I cite some areas where answers have begun to crystallize (with examples biased toward birds), in general I shall not review the literature on eco-morphological problems. Instead, I point out the key roles that have been or should be played by the scientific collection in solving the problems.

Before reviewing the topics that have become traditional among ecological morphologists, I draw the reader's attention to two areas in which, in my view, tradition has not yet been established despite these areas' importance to the field. First is the problem of establishing phylogenetic relationships among the organisms under study, without which little can be said about directions or pathways of structural adaptation. Second is the crying need for careful, quantitative correlations between behavioural and morphological characters among real groups of animals. Central as these correlations are to the theoretical foundations of ecological morphology, the field is virtually devoid of carefully documented examples from the real world. These two areas, when properly addressed, can provide substantial insight into all remaining questions I know about, within the hybrid discipline of ecological morphology.

A. The Importance of a Phylogeny

The science of classifying organisms according to their evolutionary relationships lies at the heart of systematic biology. The central role played by scientific collections in this endeavour is widely recognized (Mayr 1969; Wiley 1981), and almost goes without saying even in the present volume. We simply could not classify organisms, much less study their phylogenetic affinities, without collections of specimens to study and compare.

But why classify organisms and reconstruct phylogenies? Mayr (1969, chapter 1) provides a general response to this question. Pertinent here, however, is a more specific question: why should ecologists interested in morphology bother paying attention to the taxonomy and classifications of their organisms? After all, relationships between body form and ecological variables could be (and are, all too frequently) described and analyzed without reference to any evolutionary past, and in complete ignorance of similarities or differences among related species. Of course, this represents a static view of ecological communities and evolution, and it ignores the essential fact that every organism, population, and species is a product of its own unique history. To study the morphological attributes of an organism in relation to ecological features, but without equal attention to phylogenetic ones, ignores some potentially major constraints upon the organism's shape; the practice also fails to take advantage of indispensable information that can be contained in the evolutionary history of a group.

Questions appropriate for an eco-morphologist deal with the kinds of selective forces that can operate within communities to cause morphological *change* in a population or species. Once we address the question of change, either across space or through time, we logically are forced to make comparisons between populations: for example, we compare genetic factors, character states, localities, habitat preferences, climatic environments, or behaviour patterns, to mention a few important variables. From the observed differences, we infer that change has taken place. The problem facing an ecological morphologist, then, is to choose a proper set of units or entities to compare. The goals of such comparisons are: (1) to demonstrate that certain of the units being compared look different from certain other ones; (2) to infer that these differences resulted from *change* through time; (3) to calculate the amount and directions of these changes; and, finally, (4) to make inferences and alternative, testable hypotheses about the forces that *cause* these changes.

A common method among experimental ecologists is to place a series of identical samples of a given organism into a variety of controlled environmental settings, thereby documenting the environmental influences upon development, reproductive attributes, longevity, and other biological variables. Extending the same tests across many generations (e.g. Endler 1981) allows experimental analysis of selection itself under a controlled setting.

With only a few exceptions (e.g. James 1983), ecological morphologists cannot use these experimental techniques to study the interactions between shape and environment. Instead, we choose populations or species (taxa) we "know" to be closely related (i.e. sharing a relatively recent common ancestor), and we make our comparisons across these taxa. Conceptually, this is the same approach as the manipulations just mentioned: presumably once-similar samples are studied after some change has occurred in some of them. From the present-day differences, we learn something about how organisms responded to environmental pressures. However, the differences between this technique and true ecological experimentation are profound. First, in comparing across taxa we do not control the forces that caused the observed changes; we must infer them by means of correlations and comparisons. Second, many forces, including random chance, usually will have been at work simultaneously to cause changes among taxa over time. This complicates the task of inferring how environmental pressures affect body form. Third — and here we return to our theme — we usually have no concrete proof that the taxa we choose to compare are indeed common derivatives from a shared ancestor. The purpose of assessing phylogenies is to minimize the chance of error in this third problem area. Such errors, many of them severe, frequently are not appreciated by ecological morphologists. Two of the most conspicuous errors are illustrated schematically in Figs. 1 and 2, showing the logical necessity of establishing relationships before assessing interactions between shape and environment.

In Fig. 1, two hypothetical character states are plotted against a climatic variable for six taxa, A through F. In this example, species in dry climates are smaller and fatter than those in wet climates. This observed correlation holds irrespective of phylogenetic relationships among the taxa. However, the degree to which we can infer causality varies considerably according to these relationships. Three alternative phylogenies illustrate this point. Suppose the entire group is a monophyletic unit, with relationships as shown at the bottom (three pairs of sister species, AD, BF, CE). Regardless of the primitive conditions of any of the three plotted characters, independent and parallel *changes* (i.e. character-state transitions) must have occurred at least three times for each character. Such a repeated pattern strongly suggests that a causal relationship exists between shape and climate (although much additional work would be required to establish the relationship more firmly in this simple example).

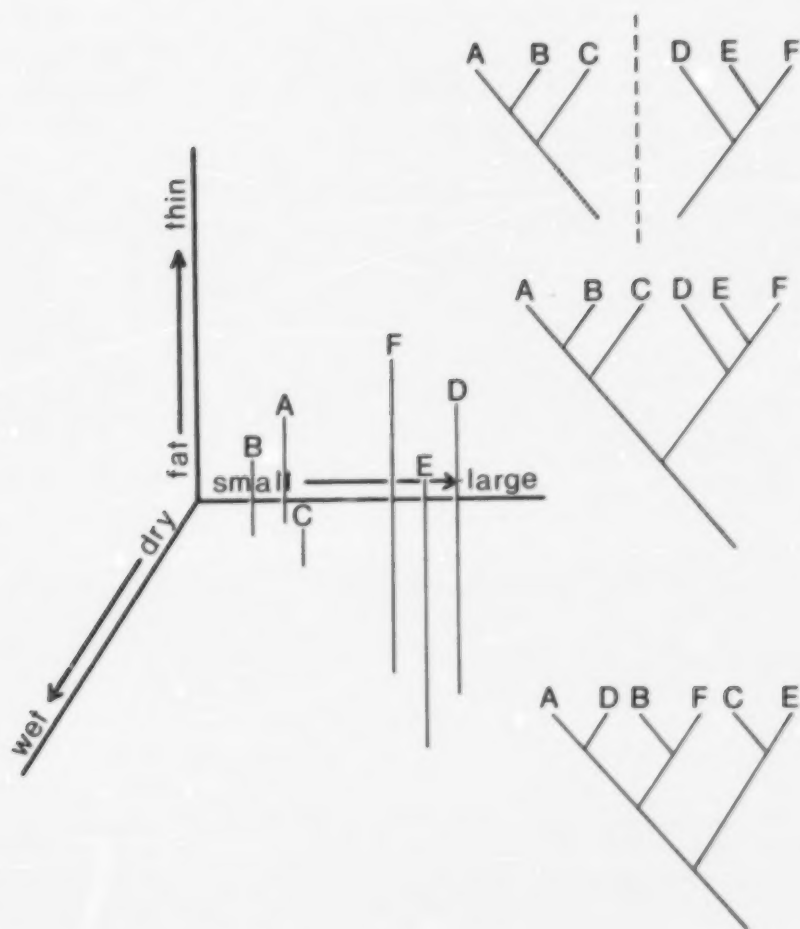


Fig. 1. To the left, a three-dimensional graph plotting three character states of six hypothetical species, A through F (vertical lines show height above lower horizontal plane). To the right, three possible configurations by which the six species are phylogenetically related. Each configuration provides a different interpretation of the degree to which shape and size are directly related to climate (see text for detailed explanation).

In contrast, suppose that A, B, and C are each other's closest relatives, unrelated to D, E, and F (uppermost phylogeny). In this case we can infer nothing from the graph, except that the group ABC, members of which happen to be small and fat, prefers drier climates than do the big, thin DEF taxa. Indeed, within each group the original correlation actually is reversed. The middle phylogeny provides suggestive but equivocal evidence for a non-spurious relationship between climate and morphology. Our resulting hypothesis about relationships between structure and climate, given the identical data set, depend entirely upon the relationships between the species we studied.

Fig. 2 illustrates another potential misuse of phylogenies within ecological morphology. This example shows that comparisons between related taxa are useful when entire monophyletic groups are considered,

but can be potentially misleading if poorly chosen subsets of that group are compared. Presented only with the data in the upper diagram, one might hypothesize that size and climatic conditions are inter-related as in Fig. 1. The correlation exists even within a group we have identified as monophyletic. However, suppose that an independent researcher (perhaps at a larger museum) studies the same group but includes additional, related species in a more completely reconstructed phylogeny (Fig. 2, bottom). The second picture not only introduces data that conflict with the correlation, but it suggests a parsimonious interpretation of the size-climate relationship not necessarily related to ecological factors (one ancestral population became large, while its sister species remained small, and a descendant of the large species colonized a wet habitat while all descendants of the smaller species remained in dry areas). Armed with an incomplete set of data on relationships and character states within the group, we might have been tempted to propose a causal relationship between form and environment that was entirely spurious.

These examples are designed to show obvious flaws in reasoning. In real examples, which usually include more complicated sets of data and more numerous and subtle environmental relationships, the flaws become far less obvious. Our hypotheses about reasons for character-state transitions, then, depend

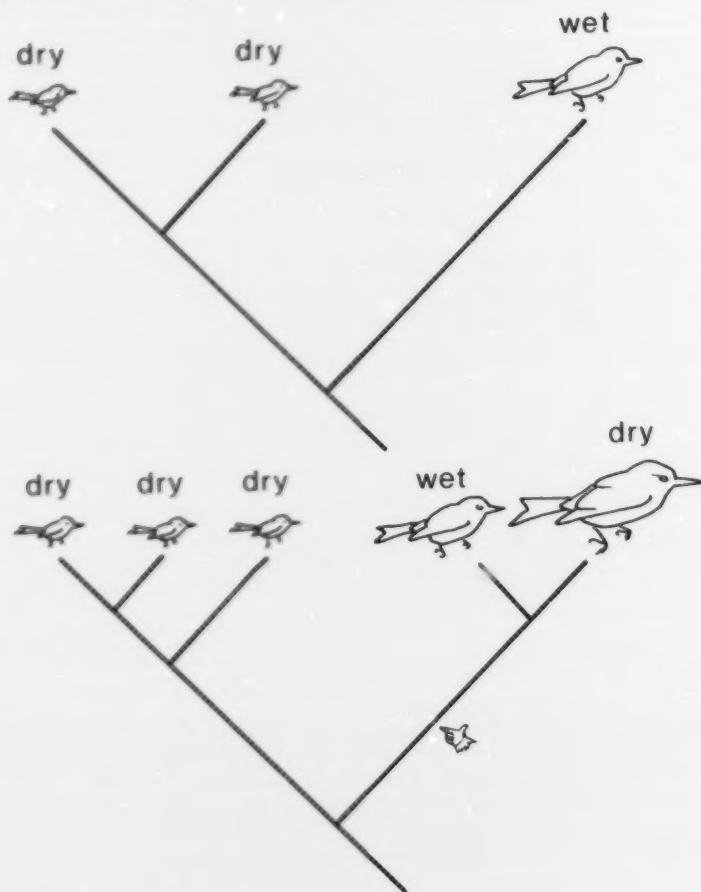


Fig. 2. Two phylogenies of the same hypothetical group of birds, the lower one including two more species than the upper. Climatic conditions occupied by each species are shown. Examination of only a part of any group (upper example) can lead to unsafe or incorrect inferences that can be refuted when the entire group is analyzed. Finger points to the taxon at which size increase presumably occurred, followed by colonization of a wet habitat by one of the two descendant species. No climatic influence upon size is implied by the lower data set.

first upon an adequate reconstruction of those transitions. Such a reconstruction is the ultimate goal of phylogenetic systematics (Wiley 1981). In this sense a defensible phylogeny represents not an end in itself (as many systematists will seem to view it) but an essential tool within larger-scale analyses of evolutionary processes and pathways (see Anderson, 1979, for a first-rate, real-world example).

Ecological morphologists hope to study the forces that produce evolutionary modification of structure. The structures they study, however, have evolutionary histories that should not be ignored. Attempting to reconstruct that history can prevent logical errors, and the exercise forces the ecologist to organize and present evidence that structural modification has indeed occurred in the first place.

B. Morphological Correlations With Behaviour

Among animals, the medium through which ecology and morphology are tied together is behaviour. Ecological variables such as food choice, habitat preference, reproductive requirements, interspecific interactions, home-range use, and various annual cycles all relate to animal structure by way of behaviour. Many such relationships are apparent even to school children: winged creatures fly while four-legged ones walk or run. Others are more subtle, though no less profound. In a very real sense, all studies of ecological morphology relate in some way to the influences of structure upon behaviour, and to the notion that behavioural shifts within ancestral populations can bring about structural modifications in descendants through natural selection.

Many ecological variables that involve behaviour frequently are measured and analyzed quantitatively in relation to morphology. Typical examples, to name a few, include relationships between diet and size of body or mouthparts (e.g. review in Hespeler, 1973), body size versus latitude (McNab, 1971) or climate (James, 1970), and various relationships between morphology and interspecific competition (e.g. Brown and Wilson, 1956; Ficken *et al.*, 1968; Grant, 1972). These and many other aspects of ecological morphology are enumerated below, particularly as they relate to the use of museum collections. But analyses such as these address animal behaviour itself only indirectly. More accurately, they reflect the results of behaviour rather than the action itself.

Given the importance of the interactions between morphology and behaviour to animal ecology, a staggering deficiency exists in the voluminous literature of this field: *quantitative correlations between morphological and directly measured behavioural variables are virtually non-existent*. To my knowledge, the literature on birds, generally at the forefront in eco-morphology, contains the few examples in which both behaviour and form were quantified and directly correlated (e.g. Ricklefs and Cox 1977). My own studies (e.g. Fitzpatrick, 1978 and in press) seem to contain the first direct plots of morphological variables against pure behavioural ones.

In the literature on birds, qualitative "correlations" between form and behaviour are numerous and generally of two kinds. They appear in the works of functional anatomists (e.g. Engels 1940; Beecher 1951; Bowman 1961; Osterhaus 1962), where muscular and skeletal structures within a group are described in detail from museum specimens, and the differences are assigned to various gross differences in behaviour (usually locomotion or feeding). Alternatively, such relationships are pointed out by ecologists (e.g. Lack 1947; Newton 1967; Orians and Horn 1969; Keast 1972), sometimes with extensive data on habitat or food choice (e.g. Orians 1981), but rarely with data on behaviour *per se*, and with only cursory analysis of form (see Chapter 10).

If, as Aristotle himself surely concluded, behaviour and form are interrelated, then we should be able to measure them so as to show the relationships as correlations, much the way the rest of ecology proceeds. Indeed, such graphs would tell us a great deal that is not immediately obvious about these relationships. An example is illustrated in Fig. 3. I refrain from exploring here all the ramifications of the relationship shown in Fig. 3, but some are obvious. Among flycatchers, relative tarsus length increases continuously along a behavioural gradient related to the use of the ground as a foraging substrate. This curve demonstrates, more precisely than in the past, a familiar functional relationship (e.g., Dilger 1956; Newton 1967). More important, plotting the variables in this fashion allows us for the first time to examine the *degree* of morphological specialization that accompanies any level of specialization along the behavioural scale. The approach allows us to ask questions about the shape of the function that joins the two variables, and to examine implications of different amounts of variance at different points along it. These plots can demonstrate certain bottle-necks or points of innovation, where substantially different levels of structural specialization accompany a given degree of behavioural specialization. In general,

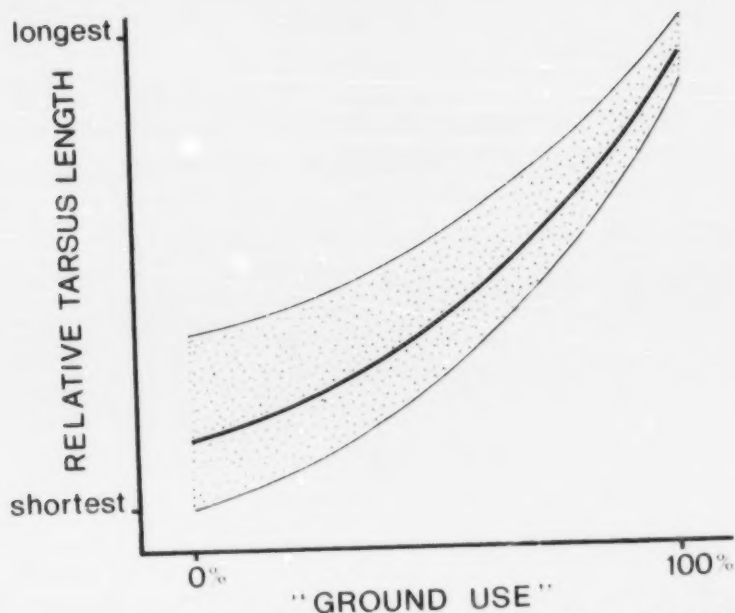


Fig. 3. A relationship between relative tarsus length within a group of birds and the degree to which those species use the ground, varying from never to always. Thick line shows the mean values at each value for ground use, and shaded area within thinner lines shows the total range of relative tarsus lengths at each value. Shape of the curve and degree of variability at each value imply some important functional aspects of adaptation (see text). This schematic figure is adapted from actual data. (After Fitzpatrick 1978, in press.)

graphs such as these allow inferences about the amounts of behavioural and morphological plasticity, and limitations to them. Such questions are of crucial importance to inferences about adaptation and specialization. Surprisingly, they have not yet been asked by eco-morphologists.

Proper construction of these graphs requires three steps: (1) choice of a group of species or populations that are known to be closely related, but containing sufficient variation to include various levels of behavioural and morphological diversification; (2) careful measurement of homologous behaviour patterns in numerous species within the group; usually, this must be preceded by a classification system that allows numerical comparisons of behaviour (Fitzpatrick 1980, MS); and (3) careful measurement of a variety of structural features for each species, choosing particularly those features that are functionally important in the behaviour patterns.

The museum collection enters this process in step one, when the proper group is chosen, its limits are defined, monophyly is verified, and phylogenetic reconstructions begin. The collection takes a back seat in step two, when behaviour patterns are recorded and classified in the field or laboratory. The collection returns in step three, as it provides the principal source of specimens for measurement.

C. Some Problems in Ecological Morphology

In this section I mention some continuing problems in which, despite substantial progress, ecological morphologists still face unresolved issues. I make no attempt at an exhaustive catalogue of such problems, but rather I mention those of special interest to me and in which the museum collection constitutes an indispensable tool. Many of the topics discussed briefly here are reviewed in more depth by Hespeneide (1973). For a technical review of morphometric methodology, and some important words of caution regarding uncritical assumptions about homology in these studies, see Bookstein (1982).

By the very nature of the term, "ecology" is a science that requires simultaneous measurements of interacting entities that compose communities. Variation within and between these entities makes com-

munities complicated, and ecology interesting. The museum collection provides a catalogued library of specimens collected over extensive space and time, thereby preserving and displaying the physical variation within communities past and present. These warehouses of natural variation permit us to measure, with laboratory precision and convenience, the physical construction of the world. The series of topics below represents an effort to organize this virtually infinite variation into bite-sized categories.

1. Allometric Variation

All questions concerning adaptive variation in structure must include analysis of the effects of size itself upon shape. Physical constraints upon growth and form have been established both theoretically and empirically (Huxley 1932; Thompson 1942; Gould 1971). Empirical demonstrations of allometric patterns are based almost entirely upon measurements of preserved specimens in collections, because such specimens permit simultaneous measurement of numerous characters, both internal and external, on the same individual. Comparative measurements typically yield bivariate plots in which single mensural characters are compared to a standard measure of size — in animals, usually body weight or length. The slope of the resulting regression, and its variance, indicate the extent to which size alone explains differences in those characters. Residuals, in turn, presumably reflect size-independent variation of greater interest to the ecological morphologist (but see Gould 1966, and 1971 for potential pitfalls).

Allometric relationships come in four principal forms depending upon the choice of specimens used for measurement. It is crucially important that the differences are recognized by the morphologist. (1) Ontogenetic series of single species can show specifically how growth affects form. Of more importance to the ecologist, they can indicate points at which certain physical characters come into functional prominence as an animal develops (e.g. Ritland 1982). (2) Allometric analysis of variation among adults within and among populations demonstrates limits to intraspecific structural variability. These limits can result from genetic factors (such as pleiotropy), from mechanical factors imposed by scaling problems alone, or from canalization in body form imposed by natural selection for an optimal shape. Evolutionary biologists still are a long way from partitioning the roles of these factors. (3) Interspecific comparisons, especially among related species, perhaps form the most informative exercises for ecological morphologists, in that the amount of variation owing to size alone usually will be less than in the two previous cases. With size removed from analyses of form, functional correlations and interpretations of structural differences become more transparent. Finally, (4) comparisons of fossil specimens permit allometric analysis within phyletic series, shedding light on structural trends and limitations through time instead of across it.

2. Intraspecific Variation

a. Sexual Dimorphism The existence of preserved specimens properly identified as to sex and locality is essential to the study of sexual dimorphism among animals, especially those in which the sex is not identifiable externally. Among the unresolved problems in this area is the possibility raised by Selander (1966) that sexual size dimorphism is a result of selection for divergence in food or foraging habits. Still needed is a more complete catalogue of the patterns of sexual size dimorphism across species, and between populations of the same species living under different environmental regimes. Bird species that show unusual sexual dimorphism in feeding structures [e.g. certain Hawaiian honeycreepers (Drepanididae), the extinct *Huia* (*Neomorpha acutirostris*), certain woodpeckers (Picidae)] frequently occur on islands (Selander 1966), suggesting that some feature of the resource base or competitor community allows a broadening of the trophic niche and selects for sexual differences. However, some dramatic sexual differences in behaviour among birds (e.g. Williamson 1971; review in Power 1980) are not accompanied by changes in morphology. As outlined above, the specific relationships between behaviour and structure need to be quantified directly among sexually dimorphic species in order to address this point unambiguously.

b. Climate and Latitude Controversy still exists about the generality and ecological implications of geographic trends in body size within and between species (see Chapter 6). Perhaps no such trend is better known or studied than Bergmann's rule, the apparent tendency for animal body sizes to be larger in

cooler climates. In 1847, Bergmann himself (translated in James 1970) discussed the rule as an interspecific phenomenon, but it later was modified to describe within-species trends only (Mayr 1963). Documentation of both inter- and intraspecific trends traditionally relies upon standardized measurements of museum specimens. They have the advantages of being numerous, being centralized into a relatively few large collections, and of bearing the precise locality of collection. Thus, they provide sample sizes from wide geographic areas that would be impossible to match by visiting all these areas personally.

The importance of climatic conditions in determining body size was stressed by Rosenzweig (1968), Power (1969), and James (1970), because climatic variables such as temperature and humidity are often strongly correlated with trends in body size. These correlations were disputed by McNab (1971) as being spurious, and he argued that changing prey size distributions better explained the geographic size trends. The matter is unresolved, and surely will require a more extensive analysis of regional size trends in a wider array of species (fewer than 20 of North America's 600 breeding bird species have been mapped in sufficient detail to indicate the regional trends in body size). The empirical end of such studies requires enormous sample sizes of measurements from numerous localities across the ranges of widespread taxa. Modern statistical analyses of the raw data from specimens include trend-surface analyses (Haffer and Fitzpatrick, in press) as well as more conventional isophene plots (e.g. James 1970) and multivariate analyses combining climatic and morphological data (reviewed in Johnston and Selander 1973; see Chapter 6).

c. Insular Trends The explosion of interest in island ecology over the past two decades occurred because islands produce natural experiments on a scale not readily reproduced on the mainland. Darwin himself realized this, and the specimens he collected on islands provided a lifetime of grist on which he could chew. Indeed, his very specimens of geospizine finches from the Galapagos Islands recently formed the basis for some important reanalyses of Darwin's procedures and findings (Sulloway 1982a & b). The world's holdings of scientific specimens collected on islands over the past several centuries take on new importance in light of recent findings of Boag and Grant (1981), who provide dramatic evidence for the speed at which natural selection can operate to change phenotypes in natural island populations. Museum collections contain specimens of species taken both on islands and the mainland at various points in time, back at least one and a half centuries. These historical specimens provide us with the only means for studying rates and patterns of phenotypic change across long time intervals (e.g., Johnston and Selander 1964, 1971).

d. Character Displacement The classic example used by Brown and Wilson (1956) to illustrate character displacement (Vaurie 1951) was shown by Grant (1972) to be inconclusive — apparently the result of two parallel clines in bill size among partly sympatric species of nuthatches (genus *Sitta*). Grant similarly showed that numerous other examples also were suspect. His demonstrations relied upon the availability of specimens from numerous localities across the ranges of the species in question. An unequivocal case requires that a sharp divergence in character size between two species occur more or less precisely at the geographic point at which the two species come in contact. Grant (1972) argued that no such clean case exists to demonstrate the phenomenon. His argument ignores the effects of gene flow between areas of sympatry and allopatry, which could cause a biologically "clean" case to be disguised as two independent clines.

McNab (1971) holds that many large-scale examples of regional trends in body size actually are large-scale examples of character displacement (*contra* James, 1970, and Rosenzweig, 1968). All authors agree that the key element in testing for true character displacement is the existence of large sample sizes of specimens from a variety of localities across the ranges of two or more potentially competing species. Ecological morphologists still have the dual chore, in even one case, of showing first that the species in question are indeed actively in competition, and then that they have actually diverged in shape in their area of contact. The world's scientific collections now hold vast stores of information on geographic distributions and morphological variation among countless such pairs of animals. It seems peculiar, therefore, that the verdict on the reality of character displacement is so slow in coming.

e. The Niche-variation Hypothesis Among the most useful aspects of good scientific collections is that they preserve large series of specimens of each species from single localities. This permits estimation of individual structural variation within single populations. Several authors have proposed that the amount of this phenotypic variation may be directly related to the breadth of a population's ecological niche (Van Valen 1965; Soulé and Stewart 1970). Some evidence for and against this hypothesis is reviewed by Hespeneheide (1973). Traditionally, the problem has been approached by separately analyzing a feature of niche breadth (e.g. size and composition of food resources used) and a functionally related morphological feature (e.g. bill size), with mixed results (Van Valen and Grant 1970). Again, the verdict on this question is not in, and again, scientific collections will play an important role in providing one. Their role, in this case, will be to provide comparative samples of different species exhibiting different amounts of intrademic variation. By identifying a sample of species, preferably closely related, which show varying amounts of variation, the ecologist can pinpoint which sets of taxa to examine in the field. Standardized analyses of niche breadth within these taxa would then yield direct data indicating whether morphological and ecological variation are related. Clearly, profound differences exist in the amount of variability even among close relatives. Relating morphological variation to behavioural variation at the individual level is the ideal procedure for analyzing this question. Unfortunately, such a technique is possible only under the most ideal field conditions, and in species exhibiting unusually pronounced individual variation (e.g. Boag and Grant 1981). The scientific collection provides an easy avenue for identifying such informative examples.

3. Interspecific Variation

a. Predator-prey Relationships As pointed out by Hespeneheide (1973), animals generally come in three trophic types: those that are either much smaller (parasites) or much larger (grazers and filter feeders) than their prey, and those that are within a few orders of magnitude of the same size (hunters). Measurements of specimens of both predator and prey are most instructive for this third category because it is the only one in which functional correlations should be expected. A variety of questions pertaining to morphology and community interactions relate to the precise size relationships between predator and prey. Do certain physical structures of the predator (e.g. mouthparts, claws, gut width) correlate more closely to prey size than does overall predator body size? What are the ways in which differences in foraging or feeding behaviour affect the slope and strength of such correlations (stressed by Hespeneheide 1971, 1975). Preserved specimens, especially those that retain their gut contents, permit extremely accurate assessment of these relationships (e.g. Voris and Moffett 1981). In comparing the diets of similar-sized species, even those that consume similar-sized prey, the taxonomic composition of those prey constitutes an ecologically important parameter. To the ecological morphologist, then, correct identification of the prey items themselves is required in many cases. Perusal of the vast literature on such studies indicates the essential role played by scientific reference collections in this exercise. The use of collections is most imperative when the prey items being analyzed consist of dismembered and partly digested insect fragments, as usually is the case among birds and many small mammals.

Careful measurements of prey size have been used to assess the variability in diet both within and among species. Voris and Moffett (1981) found evidence for prey-size selection in sea snakes by noting an increase in the lower limit of the prey-size range among larger individuals within a population. Interspecific differences in prey choice, even among similar-sized and -shaped predators, have been tied to specific differences in head and mouthpart structures in snakes (e.g. Pough and Groves 1983), a phenomenon now well demonstrated among birds (e.g. Abbott *et al.* 1977).

b. Reproductive and Life-history Implications Studies of preserved specimens in reproductive condition have been indispensable in demonstrating the relationship between size and reproductive output, especially among animals with indeterminate growth (e.g. Tinkle *et al.* 1970; Fitch 1970; see Chapter 13). Among reptiles the relationship is consistent within a species but shows differing slopes between species (e.g. Lemen and Voris 1981), indicating differences in strategies of lifetime reproductive investment. The social implications of size-dependent reproductive output have only begun to be addressed (Douglass 1977). Although theoretical and field studies of life-history strategies rely primarily upon measurements of

the living organism, scientific collections repeatedly have been used to test the hypotheses thereby generated. Features such as body size, juvenal versus subadult or adult plumage patterns (e.g. Rohwer *et al.* 1980), development of secondary sexual characteristics (e.g. Gadgil 1972), and numerous other structural characteristics are intimately tied to life-history adaptations among both animals and plants (see Chapter 11). Comparative study of all such features depends upon the existence of adequate samples of specimens preserved in collections.

c. Convergent Evolution A principal interest to ecological morphologists is the repeated, independent convergence upon similar shapes by unrelated taxa. Convergence is widely recognized as a problem to the systematist (e.g. Mayr 1969; Wiley 1981), because similar characters may or may not reflect common ancestry. To the ecologist, however, obvious cases of convergence argue strongly for the uniformity of ecological pressures and structural constraints they place upon organisms. Various aspects of the extent to which organisms have "converged" can be determined only through detailed study of size and shape, and the process is refined through the use of multivariate analyses of these data (e.g. Karr and James 1975; review in James 1982). Documenting the degree of similarity among organisms is, of course, only the first step in a careful study of evolutionary convergence. Ecologists frequently overlook the equally important need for behavioural data to support the notion that similarity reflects functional convergence rather than any other form of drift toward similar shapes (e.g. Keast 1972). The museum collection provides a vast source of comparative data for the statistical analyses of similar shapes. Still largely absent are corresponding field and laboratory studies of the similar forms needed to demonstrate that such structural similarity, in individual characters or in overall form, results from similar behaviour or surroundings.

4. Community Variation

a. Limiting Similarity and the Morphological Community How similar can species be and still coexist in a stable community? Perhaps no genre of ecological questions has stirred more debate over the past two decades than this one, first posed by Hutchinson (1957, 1959) and later refined into a set of related hypotheses by MacArthur and associates (see Cody and Diamond 1975). Among the most important keys to the problem is to state the questions as precisely as possible. What exactly is meant by "similar"? What is the proper "set" of species within which it is ecologically meaningful to pose questions about similarity? What does it mean to "coexist," and is this a quantitative condition or a qualitative one? How stable are the communities within which field "tests" are traditionally carried out? Ecological morphologists typically compare the sizes and shapes of coexisting species, examining either the size ratios between pairs of most-similar species (e.g. Schoener 1965, 1974), or the distributions of species within a morphological "hyperspace", using multivariate techniques to make comparisons between communities (e.g. Karr and James 1975; Ricklefs and Travis 1980). Studies of birds and mammals continue to break new ground in this rapidly growing area of study (reviewed in James 1982). All such studies rely upon the museum collection as a source of measurement data. Frequently, as well, the museum serves (or should serve) as a reference for the proper identification and separation of species that do or do not occur together in nature.

IV. CONCLUDING COMMENTS

In touring visitors through a major scientific collection, I am asked one question more regularly than any other: why do we keep so many specimens of each species? This, more than any other question, permits me to elaborate as best I can the very essence of why we keep collections at all. The rows and rows of preserved specimens, properly identified and labelled to locality, provide a window into the living world. As representative samples of that world, they permit geographers, systematists, morphologists, and ecologists to imagine questions and measure the answers as to how organisms became as numerous and structurally diverse as they are.

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15. MUSEUMS AND BOTANICAL GARDENS: COMMON GOALS?

P.S. Ashton

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I. INTRODUCTION

Living scientific collections span a vast range of diversity in aims and facilities, from fungal inoculates to forest trees, protozoa to whales. Clearly, curatorial methodology is equally diverse. All the same, certain needs and problems are common to all. In this brief essay I address these as they apply to botanical gardens and arboreta.

Living biological collections have their origin at that time of transition in western thought when the medieval perception of a static natural world, preordained according to religious dogma and therefore not gainfully subject to scrutiny, was beginning to erode as Galileo, da Vinci, and Copernicus questioned the traditional views of the natural world through deductions based on careful observation. While the earliest gardens and menageries were designed as microcosms of paradise on earth they were also frequently attached to medical schools and used as sources of pharmaceutical materials (Prest 1981). Even by the fifteenth century, gardens and menageries were being used to display exotic introductions, bringing to life the astonishing tales of the explorers. From their beginnings, then, they served both as a repository for scholarly investigation and as an interpretive exhibit for the public.

Subsequently, zoological and botanical gardens have followed separate paths as scientific resources. Botanical gardens rose to great prominence as testing stations during the early colonial era, but became increasingly academic and ornamental during the nineteenth century, once the major crops in international trade had been identified, and had come to command their own specialist research stations (Ashton 1981a).

Botanical gardens are currently the subject of serious scrutiny (Anon. 1972; Ornduff 1978; Ashton 1979, 1984). They are underused by scientists, and are absurdly expensive to justify purely in terms of their current use for research alone. Their administrators have, perhaps, resorted to traditional justification for their continued existence. This is not good enough. Should we keep the great gardens, or should we drastically reduce or even eliminate their scientific functions?

I will argue here that systematic living collections must play a leading part in reunifying biology but, to do this, radical changes are needed in science, and particularly in the way biologists are being trained.

II. THE USEFULNESS OF LIVING PLANT COLLECTIONS

Living collections can be treated and justified on the same terms as preserved museum collections: as reference resources analogous to libraries, though differing from libraries in the uniqueness of the individual specimen, a quality that is an integral element of the type method in taxonomy (Ashton 1981b). Botanical gardens can therefore, in theory, be the repositories of living type specimens; but how often is this done? In fact, living collections cannot usefully serve merely as complements to preserved collections.

On the one hand, plants have the advantage over animals that they can be vegetatively repropagated indefinitely. Individual living genotypes can thereby be maintained in perpetuity. On the other hand, hybridization among closely related plant species in a collection is much more difficult to prevent than among animals (Hutchins 1981).

Living collections are obviously too demanding of space, and of collecting, curatorial, and conservation effort to permit culture of a full range of intraspecific variation even for representative taxa. Living collections require constant attention. The individual organisms are undergoing change constantly, and must be repropagated periodically. Above all, and too often neglected, they require accurate standard records of provenance and (ideally) performance throughout life if they are to be of scientific value. They require taxonomic verification.

Obviously, in comparison with preserved collections, living collections must perforce be limited to restricted taxa, or aim to be synoptic rather than comprehensive. Though specialists, particularly plant taxonomists, do accumulate comprehensive living collections for their research, inspection of old specialist collections serves to demonstrate how unrealistic it is to expect that they will be maintained in perpetuity. This is particularly so for herbaceous and greenhouse material, such as the orchid collections, still impressive but once one of the world's greatest, which survive in the City of Glasgow Botanical Gardens from the days of Sir William Hooker. But even woody collections, such as extensive *Crataegus* holdings accumulated by C.S. Sargent when he was monographing the North American species, may be decimated through inconsistent deaccession policy. Indeed, with the notable exception of long-lived plants, the synoptic approach is the only practical accessions policy for permanent living collections (Raven 1979).

What then, is the value of living collections for science? It lies in all fields in which whole or living material is required, and in which a natural setting or a population is not important. The principal advantage of living collections over field observation is that they provide ready access to taxa of different provenance that have been grown side by side, under similar if not identical conditions. In those aspects of systematics in which preparation and examination is time-consuming, such as comparative developmental morphology and anatomy, reproductive biology, and ontogeny, living collections are indispensable. Corner's (1976) classic studies of dicotyledonous seeds could never have been undertaken had he not been able to observe the plants in the Singapore and Cambridge University Botanic Gardens, and thereby collect the fruit in all stages of development to observe the seeds in fresh section, for example. In studies of growth and phenology, living collections can be of value although responses can be conditioned by the artificial conditions under which the organisms are kept so parallel field studies are desirable. Thus the phenological observations of Koriba (1958) on trees in the Singapore Garden do not always match the behaviour of the same species in the forest nearby. In these and many other respects, living collections also provide an invaluable resource for refining techniques before research is begun under more expensive, hazardous, and distant conditions in the field.

From the nineteenth century, living scientific collections have been viewed more often as an ancillary to preserved collections, and used principally for taxonomic studies. They come into their own in this respect when the organism cannot be conveniently preserved in its entirety, for those characters which are lost in dried or pickled material such as colour, certain chemical characteristics, or bark and architecture in trees. A striking contemporary example has been the development of our understanding of tree architecture through comparative study of growing saplings, and of mature trees in culture (Corner 1940; Koriba 1958; Hallé *et al.* 1978). Living collections have been used for taxonomic research by botanists in particular. Some of the best monographic and revisionary work owes much to the availability of living collections for study. C.S. Sargent's studies of the trees he introduced to the Arnold Arboretum, in all stages, greatly enhanced his "Manual of North American Trees"; C.F. Symington's classic "Forester's Manual of Dipterocarps" similarly relied much on the superb collection at Kepong. An outstanding example of the combined use of field and garden for careful study of whole plants is E.J.H. Corner's "Wayside Trees in Malaya," based in large part on the author's observations in the Singapore Botanic Garden. When the book appeared in 1940, it provided newcomers to the tropics with word pictures of living tropical trees and with convenient diagnostic characters for use in the field, for the first time.

The most important function which living collections can play today in biological research is, without doubt, to provide a substrate for bridging between research in systematic biology and other branches of our science, including physiology and molecular biology. In this book (Chapter 5), George Barrowclough refers, for instance, to the complementary skills that are possessed by biochemical geneticists and systematic biologists. But how often do we work together? Fragmentation of the disciplines is, if anything, increasingly hindering biological endeavour. The rapid advances in molecular and cellular biology are but slowly being extrapolated from the handful of organisms upon which they have been used. Why did Corner's book appear so late? Systematic botany is in important respects still imprisoned by its

history (Jacobs 1980). Even now, too many taxonomic botanists concentrate their work in the museum to the extent that their work provides but a partial inadequate base for systematic research, and is often unusable in the field. The problem in large measure lies in education: too few university students have the opportunity to explore patterns of variation in a diversity of living biological material.

University living collections have often had a checkered history (see also Chapter 1). With rapid increases in the cost of the experimental sciences, living biological collections in particular have found it difficult to compete for declining funds. This is bad for science. We live in a world in which crops and farm animals are being reduced to a few major species, both of restricted genetic variability as a consequence of purposeful breeding, and where investment is concentrated in research which addresses universal biological questions at the molecular level. University living collections provide unique opportunities for extrapolating from the molecule to the organism, and from the organism to the diversity of life. The work of P.A. Thompson and his group at Kew, on the comparative physiology of seed dormancy, sets a good example. Systematic physiological and biochemical research is likewise opportune to gain understanding of the principles of tissue culture, and animal-plant and plant-fungus co-evolution. Systematic biologists familiar with living collections are the ones who must facilitate the dialogue between the disciplines, because they alone have the breadth to identify the most promising materials and approaches. When this happens, the recognized value of living collections will indeed become immense.

III. THE CURATION OF LIVING COLLECTIONS

There has often also grown up, in botanical gardens at least, an intellectual rift between curatorial staff and those scientists who use the collections. A trite explanation is that horticulturalists and botanists are each provided with a vocational training which lacks a common, broad theoretical base. It is a sad symptom of a missed opportunity for empirical and experimental scientists to collaborate, with the collections as a shared resource. When such collaboration does occur, living collections come into their own, and the basic need for a clearly defined accessions policy becomes apparent. Carefully kept records become a resource in their own right, supplemented in plants by voucher specimens of the parent, and of the various stages of life history (see Chapter 13).

Living collections are of little value in research unless documented. Large living collections pose special problems for curation. Their condition changes rapidly in time and should be monitored. They suffer from stress and disease, and treatments for those should be recorded. They demand much space, which generally requires that they be accessible to the public; the possibility of vandalism then arises. Records of previous research to which they have been subject need to be accessible (Ashton 1984).

Further, the general necessity for living collections to aim to be synoptic rather than comprehensive imposes a need for a clearly and consistently defined accessions policy for permanent collections, and clear criteria for the choice of taxa.

Living collections records therefore pose a challenge, to maintain standard descriptions which can be readily understood. As an example, the standard recording sheet used at the Arnold Arboretum is figured (Fig. 1). These records are used in association with location maps for all plants in the collections. Records are kept of the origin, nomenclature, method of propagation, and history, and of ephemeral features that have been observed. The presence of herbarium vouchers, and frequency of inspection, are noted. Computers now allow such records, previously kept on cards and therefore of restricted accessibility, to become readily available for curation and research. Curators of those collections that have kept good records have thereby gained multiple access to a mass of conveniently tabulated information for the first time.

If a plant is propagated from seed, its identity must be regarded as suspect even if collected from the wild, but it cannot be verified until it reaches reproductive maturity. An important aspect of the curation of living plant collections is therefore vouchering by herbarium specimens. The herbarium is therefore an essential curatorial adjunct to a scientific living plant collection. Where possible, herbarium collections should be made of the parent so that progeny, on reaching maturity, can be compared. More important, vouchers should be made of plants in the collections once they have reached maturity, for verification of identity. A supplementary data sheet for reproductive information on living plants is shown in Fig. 2.

Unlike preserved specimens, it is generally impractical to borrow substantial quantities of living material for research. Rather, propagules or freshly collected whole organisms must be acquired, maintained throughout the period of the research and, except sometimes in the case of rare material, disposed of.

FORMAT FOR RECORDS ENTRY TO LIVING COLLECTIONS FILE

ACCESSION NUMBER: _____ (14)

BOTANICAL NAME: _____ (50)

TYPE SPECIMEN? IF YES, TYPE ASTERISK: MEMORIALIZED TO: _____

LOCATION: _____ NO. OF PLTS. (ORIG.) (CURRENT)
IF MASS: _____

DATE PLANTED: MO/YR or as SP 79: _____ (5)

NO. RECD: _____ (3) HOW RECD: _____ (10) DATE RECD: _____ (10)

SOURCE: _____ (50)

PRIMARY SOURCE: _____ (50)

COLL. DATA: WILD OR CULT? _____ (4) LOCALE: _____ (46)

COLLECTOR'S NAME AND COLLECTION NO.: _____ (25)

SPECIAL CHARACTERISTICS: FOLIAGE: _____ (50)

SPECIAL CHARACTERISTICS: FLOWERS OR FLOWERING TIME: _____ (50)

SPECIAL CHARACTERISTICS: FRUIT OR FRUITING TIME: _____ (50)

SPECIAL CHARACTERISTICS: GROWTH RATE OR HABIT: _____ (50)

SPECIAL CHARACTERISTICS: HARDINESS: _____ (50)

SPECIAL CHARACTERISTICS: OTHER: _____ (50)

LAST CHECKED ON GROUNDS: INITIALS MO/YR: _____ (9)

IDENTITY VERIFIED BY TAXONOMIST: INITIALS MO/YR: _____ (9)

PREVIOUSLY IDENTIFIED AS: _____ (50)

CHROMOSOME NUMBER: AS PUBLISHED: _____ (6) THIS PLT.: _____ (6)

HERBARIUM DATA _____

COMMENTS: _____ (150)

Fig. 1. Format for the standard recording sheet used at the Arnold Arboretum of Harvard University.

SUPPLEMENTARY DATA SHEET

FAMILY NAME: _____ (15)
BOTANICAL NAME: _____ (50)
AUTHOR AND REFERENCE: _____ (35)
PREVIOUSLY IDENTIFIED AS: _____ (50)
NOMENCLATURE VERIFIED: INITIALS MO/YR: _____ (9)
COMMON NAME: _____ (30)
NATIVITY: _____ (25)
INTRODUCED BY/HYBRIDIZED BY: _____ (10)
CULTIVAR OF WHAT SPECIES: _____ (15)
IF HYBRID: SEED PARENT: _____ (15)
 POLLEN PARENT: _____ (15)

INTRODUCED TO CULTIVATION IN THE U.S. BY ARNOLD ARB.? IF YES, TYPE ASTERISK

Fig. 2. Format for the supplementary data sheet, with emphasis on reproductive information, used at the Arnold Arboretum of Harvard University.

Scientific gardens, zoological or botanical, therefore need space for temporary collections for observation or experiment. Plants have the advantage that genotypes can be replicated by vegetative propagation for research purposes. Also, comprehensive collections may be temporarily accumulated by the monographer.

IV. BOTANICAL GARDENS AND CONSERVATION

Taxa threatened with extinction must be obtained for research from other collections when possible. The *ex-situ* culture of rare and endangered taxa is therefore an important auxiliary function of living collections (Walters 1977; Thompson 1979).

There has been much discussion of the conservation value of *ex-situ* cultures. It is generally agreed that *ex-situ* conservation is hazardous, and a poor substitute to conservation within the original location and habitat (Jacobs 1978), but it is increasingly becoming the only alternative available. The past history of living collections, even over the brief four centuries of their existence, does not give grounds for optimism that *ex-situ* populations of organisms are likely to persist in culture once their native habitat is destroyed, except in the case of the larger terrestrial vertebrates and of long-lived plants. The popularity of seed banks as means of long-term conservation is similarly unduly optimistic, though their short-term value is undisputed. The maintenance of threatened organisms in culture for research purposes should be encouraged though, for greater understanding of the growing requirements and reproductive biology of the organism can be obtained, and propagules thereby obtained for distribution and reintroduction in the wild (see Fig. 2).

V. BOTANICAL GARDENS AND HIGHER EDUCATION

The shortage of biologists with experience of living collections as research tools underscores that education must be one of the collector's major functions. With the decline of formal training in classical

taxonomy at universities, independent living collections provided with the facilities necessary for taxonomic research, including preserved collections, must increasingly take over the training of curatorial taxonomists. It is vital that living and preserved collections be used together in curatorial training if competent broad-based taxonomy is to flourish.

Collections associated with universities provide the forum for training, not only in the more theoretical aspects of systematics, but for scientists other than taxonomists, in the bases of biological diversity and the systematic method. They give opportunities for familiarizing such students with the use of a breadth of living material, and with studies involving the whole living organism (Walters 1979). The failure to use collections for instruction in a stimulating manner must be recognized as one reason why systematic biology has dropped from curricula in many colleges.

VI. EPILOGUE

In this essay I have taken a literal definition of a botanical garden, as a living plant collection established for botanical study or instruction. Basic requirements are that the plants be properly named and documented, curated in such a way that as many of their characteristics in nature are manifested as is possible, and arranged in the most appropriate order for the purpose of the particular collection. Beyond this, design, accessions, and curatorial policy will depend on the mission of the individual garden. Emphasis may be on research, or on instruction. The scope of either may be broad or narrow; research may be applied or basic; instruction may be at the university level or for public interpretation, and policy must be designed appropriately. In recent years though, the term Botanical Garden seems to have acquired a certain *cachet*, and all manner of plantings, often horticultural or merely ornamental in intent, have been given the title in order to attract public support. Obviously, this chapter has no relevance to these gardens.

Much that concerns botanical gardens applies equally to zoos. Living animals require yet more attention than plants, and are generally impossible to propagate asexually. On the other hand, the scope of comparative and systematic experimental research for which zoos can be used may be yet broader than for botanical gardens. They include aspects of behaviour and nutrition, for instance, unique to the animal world. Indeed, the rapid expansion of physiological and biochemical research at San Diego, New York, and other major zoos is demonstrating potentials which botanists have too seldom exploited.

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16. MUSEUM COLLECTIONS: PERSPECTIVES

HENRI OUELLET

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I. INTRODUCTION

A. The Past

The collection and preservation of biological material have occurred throughout history because man has always used animals and plants for essential purposes such as food and clothes, medications and other domestic uses. However, few records have been left of other uses for animals and plants, except for religious reasons. It was not until the seventeenth century that specimens of plants and animals were collected and preserved for less utilitarian motives. Even in early records of human history, animals and plants were often shown in pictographs such as those by our Cro-Magnon relatives. Later the Egyptians depicted many animals and plants in the abundant illustrations of their daily life. Although the purposes of this art are not clear and may have been mainly religious, it provides an actual geographic and historical record of a number of animals and plants. The Egyptians also preserved animals as mummies for religious reasons.

In the seventeenth century collections of animals started to be made for more intellectual pursuits. Such collections represented assemblages of curiosities which were occasionally displayed to the public, but which were primarily shown to a limited audience among the cultural elite of the time, or to groups of individuals interested in the subject. In this fashion, the first natural history museum was established in 1683 in Oxford, England. It was followed by many others during the eighteenth and nineteenth centuries. However, the richest collections of plants and animals were made by keen collectors and naturalists who often had considerable means and thus could run, independently, their private "cabinets" of natural history. The cabinets flourished in Europe and often contained large collections which have since become the predecessors of several of the most important scientific collections now in existence. They comprised primarily collections of birds, mammals, insects and, to a lesser extent, shells. The larger of these cabinets contributed much during the nineteenth century to preserving extensive collections of exotic animals and plants and to providing unique first-hand information on distribution, diversity and, above all, to creating a broad basis upon which classification systems have developed and evolved.

Until the middle of the latter half of the nineteenth century large collections of animals and plants were made for taxonomic or systematic studies, in addition to providing material for exhibition purposes, which would contribute to an increase of knowledge for the public on animals and plants from their own country and from abroad. These are still goals of modern museums, although there has been recently an unfortunate tendency to replace, too often, real specimens with models, photographs or other visual material in public displays, even in very large museums.

By the beginning of the twentieth century, considerable biological collections had been assembled in private collections or in public museums. The former have often been incorporated into holdings of the more important public museums because the latter were expected to have the necessary resources to main-

tain large collections *ad infinitum*, and to make them available for research or display. These collections have served as the basis for most of the classification systems currently in use, and continue to be a source of important documentation for biologists, notwithstanding the fact that they are still as essential in modern taxonomic and systematic studies as they were in the past. Their role is periodically redefined (Berlioz 1958) or questioned (Ricklefs 1980, 1981).

B. The Present

The contribution and value of existing collections cannot be denied because they have been and will continue to be the cornerstone of modern taxonomy and systematics. The importance and role of traditional collections (notably ornithological) in contemporary biology have been questioned (Ricklefs 1980), but strong arguments in their favour have been made (Berlioz 1958; McKittrick 1981; Olson 1981; Ricklefs 1981), even in the light of more modern methods of research and analysis.

For non-taxonomists and non-systematists, biological collections, even older ones which contain only scanty label data, constitute a vast and rich source of information. Modern biologists are sometimes critical of the value of older collections in view of current research trends in systematics, which incorporate biochemical or karyological data. Nevertheless, the value of older collections remains, for providing fundamental information and basic data for research projects which are oriented differently than many current studies. Traditional museum collections are essential in the study of biogeography, historical changes in distribution, nomenclature, ecological distribution and changes, geographic variation, and morphology among others (see previous chapters in this book). However, certain sorts of critical data can only be extracted from older collections by individuals trained in the use of specimens. Guidance and advice must often come from collection curators who are trained taxonomists or systematists, and who have a responsibility in fulfilling this function.

Millions of biological specimens exist in the museums of the world, and most are available for research. Nevertheless, it is essential to continue to acquire new material and expand existing collections. Even if all existing specimens of a given species were gathered in one institution for a particular study, we would soon realize that their geographic representation is inadequate due to inadequate sampling of the species' known range, or to statistically inadequate series for any given locality; that temporal representation is inadequate with samples for only brief portions of the annual cycle; that certain age groups or stages of development are not represented; that the sexes are not equally represented; that certain colour patterns or phases are too few; that certain colours have faded with time; that essential reproductive information is lacking; and so on.

II. COLLECTING AND CONSERVATION

A. Justifying Collecting

These are only some of the reasons why curators and scientists must continue to expand the collections in their care. It is also their responsibility in doing so to improve and maximize the information potentially available with each specimen: most older specimens can yield only a limited amount of information because some basic data, which could have been recorded easily when specimens were collected originally, do not appear on labels. Curators and collectors must be rigorous, precise, and accurate in recording whatever information is required for their specimens: data must not only be precise and perfectly accurate, but legibly written on labels; and labels should contain as much information as possible in addition to the basic essential information which makes a specimen minimally useful now, and which will make it valuable in the future. When expanding their collections and filling geographic gaps, or completing adequate series of specimens, curators must capitalize on each specimen collected and transcend their own immediate needs. They have the responsibility of being aware of all the preservation techniques in use, and of attempting to preserve as much of a specimen as possible, after the basic requirements have been fulfilled, by using as many of the other techniques as feasible. Parkes (1963) has pointed out that older collections are often inadequate when one wants to investigate some aspects other than systematics or taxonomy. In many cases, if additional details had been recorded originally on the labels, those specimens could have provided the required information. An avian systematist has only to dream for a mo-

ment of the wealth of material that could be available for current studies if it had been possible to preserve avian tissues, or skeletons, for only 50% of the bird specimens collected and preserved since 1900!

Countless habitats and even entire ecosystems are changing, diminishing, or vanishing, trends that present a serious dilemma to curators and scientists. Part of their responsibility is to salvage as much material as possible before a habitat or an ecosystem is destroyed, and to preserve the specimens in the best possible ways for eventual study (this includes rare and endangered species in captivity or cultivation). On the other hand, certain curators and scientists feel that it would be irresponsible to procure specimens from such habitats and ecosystems. Historical facts, the rarity of specimens of past and destroyed ecosystems and habitats in existing museum collections, and the rapid decline often followed by the disappearance of endemic plant and animal populations, work in favour of the first alternative. However, in all cases, every effort must be made to obtain all data possible on specimens collected in such circumstances, on their behaviour, on their ecology, and on the entire ecosystem before it is modified beyond remedy or has disappeared. Considering the new techniques of analysis developed during the last 15-20 years, samples ought to be collected with new requirements in mind, including the preservation of animal or plant tissues by cryogenic means, which could allow also analyses through methods yet to be developed.

Although the collecting of research specimens appears to be in conflict with a conservation philosophy, it is not, because the majority of museum curators and scientists are often deeply committed to conservation and involved in various aspects of conservation and its promotion. In many instances, they are the only experts on particular groups and most of them are in a privileged situation to advise regulatory or conservation agencies on measures and actions necessary to preserve species, groups of species, or even an ecosystem. In many instances, the information required to define conservation programs can only be obtained from existing or recently collected specimens. Although collection and conservation appear contradictory to many people, answers to the solution of conservation problems can often be obtained only from specimens. It is the role and responsibility of museums to inform the public and sometimes the legislator about this apparent conflict and insure that both understand their important role in conservation.

B. Limiting Legislation

There is increasing pressure from a limited public against the collecting of plant and animal specimens, particularly birds. There have been abuses in the past but major associations of specialists such as the American Ornithologists' Union (1975) have issued recommendations and codes of ethics on collecting. Opposition, even from a small segment of the public, is a matter of serious concern to curators and scientists because if it continues to grow it may irremediably affect collection development and hamper seriously, even stop, much of the systematics and evolutionary research for which freshly collected material is essential. We, curators and scientists, may be responsible to a great extent for the present situation in that we have been unable (or did not want) to inform the uninitiated of our activities and explain why we are collecting, why we are assembling large series of specimens rather than work from one specimen only, why we need to expand our collections and how everyone, even future generations, will benefit from our current collecting and research activities. In spite of the fact that some people will continue to oppose more strongly the collection of animals and plants because of a personal commitment against killing, we must explain more clearly and more convincingly our views, detail our needs and, finally, share with the public the results of our research when appropriate — because "our" needs are the public needs, ultimately. In this area of our activities we have an enormous public relations challenge to which every museum curator and scientist has the duty to respond.

As a result of pressures from a conservation-minded public, legislation has become more strict in many countries, states, provinces, and territories. Consequently, collecting is now regulated fairly strictly for most groups of animals and, to a lesser extent, plants. International circulation of specimens, through loans or exchanges, is equally regulated by international agreements. In spite of the fact that regulations increase considerably the amount of paperwork and the delays involved in shipping and receiving specimens, these regulations should be supported by all collection curators and scientists because they are the safeguard of authorized movements of specimens in the international museum community.

Permits are no longer issued in most places for general collecting, but only upon submission of a detailed collecting program where the number of specimens required is listed by age, sex, locality, etc. Again, these requirements increase the amount of paperwork, considered by many as unnecessary. It is essential that museum curators faithfully adhere to those requirements to maintain (or regain) credibility in the eyes of law-enforcing agencies and the public in general.

C. Future Expansion

Most museum curators and scientists agree that research collections should expand to provide larger series of better documented specimens, so it is useful to examine the direction(s) of future collection expansion. As a fundamental principle, current collections should build and develop on their existing strengths rather than expand in totally new directions. However, there may be valid reasons why some duplication of material can be useful, in insuring that representative material of existing species of plants and animals, when located in various museums, has a better chance of avoiding total destruction in case of disasters. Collections should also include as complete a representation as possible of an entire taxon for comparative and reference purposes, thus avoiding the risks of shipping valuable specimens. Consultation among curators in a given field is an essential step before any extensive collection expansion is undertaken, to minimize duplication, particularly when efforts are concentrated on defined geographic areas or when research is undertaken on closely related topics or groups of taxa. Provisions must also be defined so that all specimens are used in the most effective way, and so various parts of a specimen are preserved. It is important to obtain more information on each specimen: there is a need to improve on ecological information, to note physiological condition of the specimen, to use photography or accurate written descriptions of colouration or shape, to collect internal and external parasites, and so on. By expanding the information associated with specimens we can enrich and expand museum research programs of the future.

III. NEW COLLECTIONS: NEW TECHNIQUES

New methods in taxonomic and systematic research require specific procedures for the preservation of the entire specimen or parts or tissue samples (Barrowclough 1983; Corbin 1983; Ferguson 1980; Macgregor and Varley 1983; Shields 1983a, 1983b; Sibley and Ahlquist 1983). These methods include chromosome banding, electrophoresis, and DNA-DNA and DNA-RNA hybridization. Exciting and valuable results in confirming existing classifications, or in providing strong evidence in support of new hypotheses and classifications have been obtained. Undoubtedly, as the present methods become more refined and as new methods are developed, such as the use of old specimens in biochemical analyses (Ryder 1983), collecting and preserving techniques will become more exacting. In view of the intense activity on material suitable for biochemical analyses, and of the greater demand for it, museum curators must become familiar with new preservation techniques, even if they are not engaged in biochemical systematics themselves. Curators must also familiarize themselves with long-term conservation techniques of fresh material such as tissue, blood, proteins, etc., so that no opportunity is neglected to improve collections and to ensure that such specimens are kept under the best possible conditions for future use.

More conventional preservation and conservation techniques must not be neglected, however, because specimens prepared by such methods will continue to be widely used. However, museum curators must continue to explore new ways of making preparation techniques more efficient, and to test new preservatives, chemicals, and curatorial methods which may become available. Curators must be searching for new ways which may bring about a significant improvement in current techniques. Indeed, would it not be a major contribution if a chemical were available for ichthyologists to preserve their specimens without the loss of colour?

IV. OLD COLLECTIONS: NEW TECHNIQUES

Existing collections are widely used for conventional biosystematics research, and new uses for existing specimens are frequently developed and proposed (previous chapters of this book; Ricklefs 1980; Ryder 1983). Older specimens can now be used in biochemical analyses in some instances (Ryder 1983), but can always be referred to in research on behavioural ecology or on ecological adaptations. Curators must continue to stress the importance of the specimens in their care for biogeographical and ecological research, and to emphasize the importance of collections as source material in the identification of animals or plants. Curators must also partake in the training of future systematists and taxonomists by providing advice and direction, and by giving opportunities to their successors to familiarize themselves with curation techniques and every aspects of their collections. It is equally important that general

biologists, ecologists, and environmentalists become aware of the existence and importance of museum collections for their research. Only museum curators can accomplish this task competently. Similarly, nobody is better equipped than museum curators to inform naturalists and the general public of the importance of research collections. In general, most museum curators have failed miserably in this. It is undoubtedly as a result of these shortcomings in communication that collections are often viewed as not important, or even useless, by a segment of the public. Collectively, museum curators must become more imaginative and must develop strategies to convince the public at large of the value and importance of their collections and research. At a time when resources are at a premium, museum collections must be perceived positively by the public so that the resources required for their curation and development can be assured.

Museum curators have an enormous responsibility to ensure that their collections are properly curated, maintained, rationally utilized, and expanded appropriately. The burden of this responsibility must be shared by museum directors or administrators, trustees, and governmental, public, or private bodies which control and support museums. Museum directors, if not scientists themselves, must understand what the curators are trying to accomplish, help them in defining objectives on curation and collection expansion, provide full support on mutually agreed mandates and objectives, voice the concern of the curators to higher levels of administration, and seek the necessary resources from the appropriate authorities.

The private, public, or governmental authorities on the other hand, once they have accepted and approved the mandate and objectives of the museums they sponsor, including collection and expansion plans, have an obligation to provide those institutions with the resources required to fulfill their objectives. Too often, for economic reasons and pretexts, museums have been deprived of essential resources which have caused stagnation in research and in collection curation and development. This responsibility must be assumed fully by the appropriate authorities because they, and nobody else, have the ultimate responsibility of ensuring that the heritage of a nation, a country, a state, or a province is adequately preserved.

In conclusion, mechanisms of animal and plant evolution, relationships within animal and plant groups, systematics and taxonomy of animals and plants, and many other research areas in biology, have been studied in the field and laboratory, and from the examination of museum collections of preserved animals and plants. The results obtained by scientists have vastly improved our understanding of organismal biology and its organization. Although much has been accomplished much remains to be discovered, using both traditional methods of research, and by the experimentation and development of new techniques. This is a major role and responsibility of present museum scientists and curators.

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